

TRANSACTIONS OF THE
ROYAL SOCIETY
OF SOUTH AUSTRALIA
INCORPORATED

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**THE ASCIDIANS OF SOUTH AUSTRALIA III.
NORTHERN SECTOR OF THE GREAT AUSTRALIAN BIGHT
AND ADDITIONAL RECORDS**

BY PATRICIA KOTT

Summary

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An account is given of 58 species of the Ascidiaceae from South Australia, of which 7 species are new, including two assigned to new genera in the sub-families Euherdmaniinae and Botryllinae.

Records of 22 species from the northern part of the Great Australian Bight are the first from that area and suggest that the ascidian fauna there has a considerable endemic component. Many of the species common in other parts of the Flindersian marine faunal Province have not yet been recorded from this location.

Introduction

This account of the ascidian fauna of South Australia is based on the following collections: (1) from the northern part of Spencer Gulf (made in connection with environmental studies in that area); (2) from the northern part of the Great Australian Bight (made in connection with an experimental Prawn Trawl Survey, Explorer); (3) from Investigator Strait (collected by J. Watson) and from West Island; (4) additional collections from Elliston Bay at the eastern end of the Great Australian Bight (collected by S. Shepherd). The report is supplementary to previous papers on the South Australian ascidian fauna (Kott 1972a, 1972b). It includes records of 57 species, including 7 that are new to science. Two of these new species have been assigned to new genera in the sub-families Euherdmaniinae and Botryllinae. Four species are newly recorded from South Australia.

The occurrence of 6 new species in the northern part of the Great Australian Bight suggests an unusually high endemic component for the ascidian fauna of that area, and its zoogeography is discussed.

Type material is deposited in Australian museums as indicated by the abbreviations AM (Australian Museum), NMV (National Museum of Victoria), QM (Queensland Museum), and SAM (South Australian Museum).

All available collection data for the specimens discussed are given in the Appendix.

Order ENTEROGONA

Suborder APLOUSOBRANCHIA

Family CLAVELINIDAE

Subfamily CLAVELININAE

Podoclavella cylindrica (Quoy & Gaimard).

Kott, 1972a: 5 (synonymy); 1972b: 167.

New Records: Tipara Reef (Spencer Gulf); on reef NNW Douglas Bank (upper Spencer Gulf).

Subfamily HOLOZOINAE

Distaplia australiensis Brewin, 1953: 61. Kott, 1957: 95.

New Records: upper Spencer Gulf (Stn D5).

Previous Records: Tas. (D'Entrecasteaux Channel and southern Tasmania).

Description: Colonies consist of a rounded head on a short cylindrical stalk. There is a single terminal common cloacal aperture and the zooids are arranged along either side of the cloacal canals that radiate from this aperture and extend down the length of the head. There are about 12 fine longitudinal thoracic muscles. Ten stigmata are present in each of the four rows and these are crossed by fine parastigmatic vessels. There are 8 rounded stomach folds. The gonads extend, from the pole of the

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gut loop, into a short posterior abdominal extension separated from the abdomen by a short neck. Seven to 8 elongate testis lobes are arranged in a circle with their long axes parallel to one another to form a barrel shaped mass. The vas deferens, extending from the distal end of the centre of this mass, passes around it into the abdomen. There is also an ovary in the posterior abdomen.

Remarks: The colonies are identical with those previously assigned to this species. The zooids differ from those described by Brewin in the lesser number of stigmata in each row. Kott (1957) has reported some variation in this character and the differences are not regarded as significant. The presence of a parastigmatic vessel crossing the rows of stigmata has not previously been observed, but since this is very delicate it could have been overlooked.

Sycozoa pedunculata (Quoy & Gaimard). Kott, 1972b: 170; 1972d: 234 (synonymy).

New Record: upper Spencer Gulf (Sta B4).

Atapozoa marshi Brewin, 1956: 31. Kott, 1972b: 168.

New Records: Investigator Strait (Stns Y5, Z6).

Description: The specimens are of the usual form with a long cylindrical head terminating in a rounded point. The shorter fleshy stalk is almost the same diameter as the head. The colony from Sta Z6 is the largest yet recorded, measuring 17 cm of which the stalk is only 5 cm. The minute zooids are present in the surface layer of test with long posterior abdominal stolons penetrating into the centre of the lobe. There is the usual brown pigment patch over the anterior end of the endostyle.

Family POLYCITORIDAE

Polycitor giganteum (Herdman). Kott, 1972a: 9 (synonymy); 1972c: 244.

New Records: northern Great Australian Bight; West I. (Amphitheatre Rock).

Family POLYCLINIDAE

Subfamily EUHERDMANINAE

Euherdmania australis Kott, 1957: 103; 1972b: 172.

New Records: Elliston Bay (outside bar); Investigator Strait (Sta Y5).

Description: The colonies are formed of the usual long club-shaped lobes joined basally. Each lobe is composed of a single zooid covered by its own separate sheath of sand-

stiffened test. There are 9-11 rows of 27-28 stigmata, each row crossed by a parastigmatic vessel. A pointed papilla is present in the middle of each primary transverse and parastigmatic vessel on both sides of the body. The internal wall of the stomach is arranged in longitudinal and transverse glandular ridges rather than folds.

Ritterella herdmania Kott, 1972a: 11 (synonymy); 1972b: 172; 1972c: 246.

New Record: Elliston Bay (outside bar).

FIG. 1

Description: The present colonies are smaller than usual and sometimes each lobe contains only a single zooid. The lobes are the usual spatulate, long, narrow-stemmed form. Each zooid has 5 rows of about 5 stigmata but there are no parastigmatic vessels, and a single papilla is present in the middle of each transverse vessel. There are only single rows of testis follicles in the posterior abdomina. There are 1-4 embryos in the peribranchial cavity.

Larvae are very small, 0.3 mm long. They have 3 median ampullae that alternate with the papillae, and double rows of vesicles that extend around the anterior aspect of the larvae on either side of the papillae and ampullae and extend posteriorly along either side of the dorsal mid line. There is also a paired series of vesicles that extends postero-ventrally (Fig. 1).

Remarks: This species has been taken from Elliston Bay (Kott 1972b) in May 1971, and the present colonies were collected in the previous February. Only the latter are sexually mature and contain larvae. It is not clear whether the colonies taken in May were newly settled forms, yet to reach reproductive maturity, or whether they were older colonies that reproduced earlier in the year. However, the species appears to reproduce sexually at the end of summer. Collections from Port Hacking, N.S.W. (Kott 1972c) indicate that there, although new lobes were being added to the colonies at the end of August, the species disappeared during the summer and did not return until autumn. Recolonising stock must therefore exist off Port Hacking, which reproduces sexually at the end of summer or early autumn, i.e. a similar seasonal cycle to that occurring at Elliston Bay.

PATRIDIUM n. gen.

Zooids completely embedded with both apertures opening separately to the exterior and without colonial systems. Internal longi-

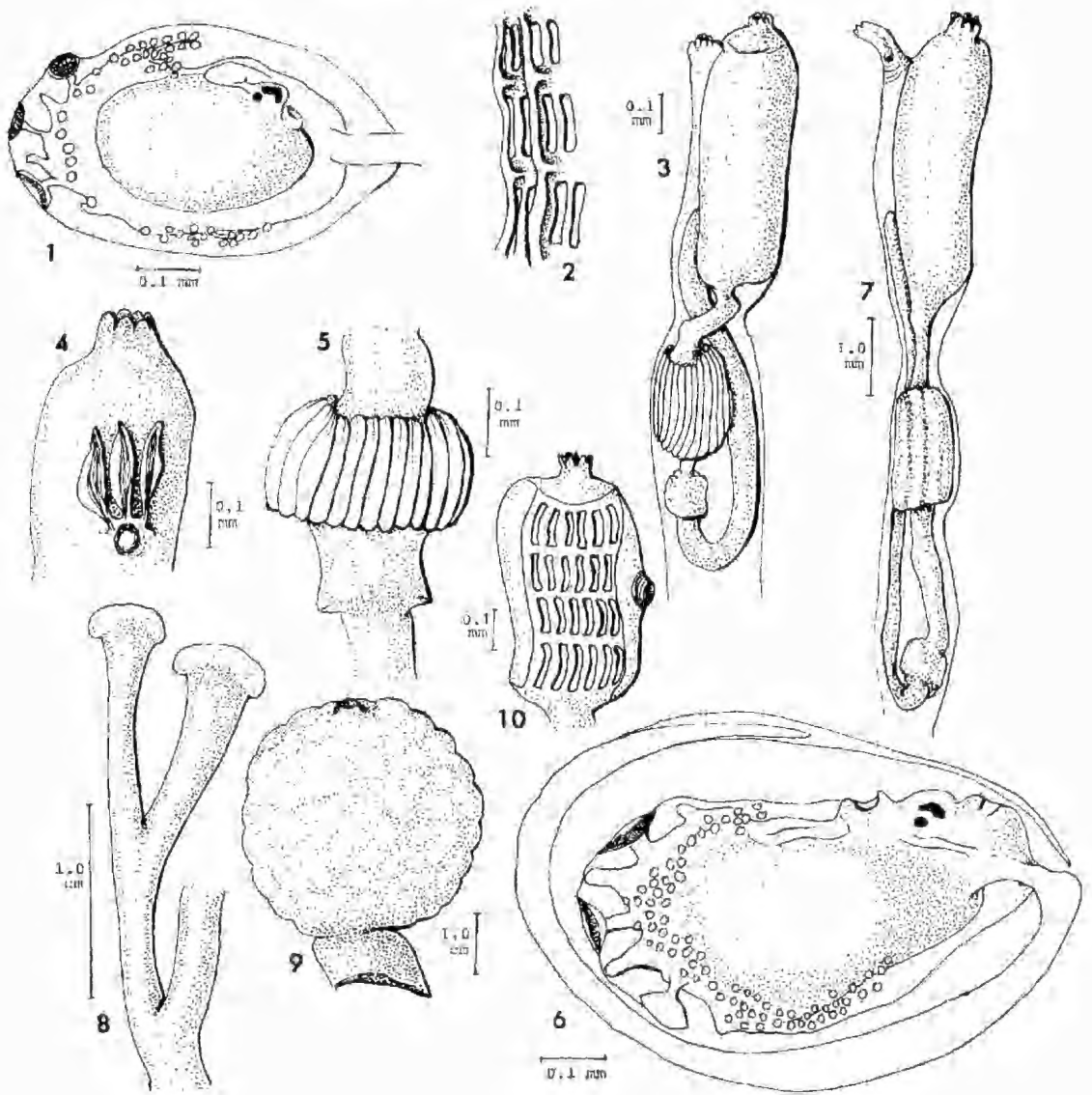


Fig. 1. *Ritterella herdmaniae*. Larva.
 Figs 2-3. *Patridium pulvinatum*. Fig. 2.—Portion of branchial sac showing internal longitudinal vessels. Fig. 3.—Thorax and abdomen of adult zooid.
 Figs 4-6. *Aplidium foliorum*. Fig. 4.—Dorsal aspect of interior portion of thorax showing tripartite atrial lip. Fig. 5.—Stomach. Fig. 6.—Larva.
 Fig. 7. *Aplidium pronum*. Thorax and abdomen of adult zooid.
 Fig. 8. *Aplidium digitatum*. Portion of colony.
 Figs 9-10. *Leptocliudes volvus*. Fig. 9.—Colony. Fig. 10.—Thorax.

tudinal vessels are present in the branchial sac. The stomach is folded. Gonads are present in the thread-like posterior abdomen, the testis follicles arranged in a double row and the ovary present just anterior to the testes. The heart is a U-shaped tube at the distal end of the posterior abdomen.

Remarks: Only two genera of the subfamily Euherdmaniinae are known in which either longitudinal vessels or their vestiges are retained in the branchial sac. These genera are *Tylobranchion* Herdman, a monotypic endemic antarctic genus (see Kott 1969), and *Protopolyclinum* Millar, in which 3 species are known,

viz. *P. pedunculatum* Millar, 1960, from New Zealand; *P. sabulosa* (Millar, 1963), from Port Phillip, Victoria; and *P. claviforme* Kott, 1963, from Eden, N.S.W. *Tylobranchion* retains some primitive characters in the presence of the heart half way down the posterior abdomen, and a large ovary posterior to the bunched testis follicles. In *Protopolyclinum* the stomach does not have longitudinal folds and the testis follicles are bunched in a short posterior abdomen as in *Polyclinum* spp. The present genus bears the same relationship to *Aplidium* as *Protopolyclinum* bears to *Polyclinum*. It differs from both *Protopolyclinum* and *Polyclinum* in the presence of stomach folds and in its long thread-like posterior abdomen in which the testis follicles are arranged in rows; it is these characters that relate it to *Aplidium*. It differs from *Ritterella*, also in the subfamily Euherdmaninae, in the presence of the longitudinal vessels, and the absence of parastigmatic vessels in the branchial sac. *Ritterella* is usually further distinguished by the presence of 5 primary rows of stigmata, although these are often subdivided by parastigmatic vessels. The restricted number of primary rows of stigmata suggests that *Ritterella* may be more specialised than *Patridium*, which demonstrates primitive affinities in the presence of a large number of rows of stigmata as well as in the retention of the inner longitudinal vessels.

***Patridium pulvinatum* n. sp.**

Type Locality: northern Great Australian Bight (32°24'S, 133°30'E), 42 m deep, S.v.1973; *P. Symond.* *Holotype:* SAM, E 1035.

FIGS 2, 3

Description: The holotype only is available. It is a circular cushion, 6 cm in diameter and 2 cm high, more or less flat topped and with rounded borders. It appears to have been sessile and attached by a small area in the centre of the basal surface although there could have been a short stalk in this position. The test is very soft and semi-transparent, generally without sand or other adherent foreign particles except for a small sandy area at one side of the basal surface. The zooids are thread like, the thorax and abdomen together are 1.5 mm long and the posterior abdomen about 4 mm. They open all around the upper surface and the posterior abdomina project down into the centre of the colony. The apertures are both 6-lobed. Fine longitudinal muscle bands extend along

both sides of the zooid for its whole length. There are about 25 rows of 16 short, oval, stigmata; rather tall papillae are present on the transverse vessels and these support longitudinal vessels running the whole length of the branchial sac. The longitudinal vessels are crowded, being separated from one another by an interval equivalent to the width of about one and a half stigmata. The oesophagus is fairly long and there is a voluminous stomach about halfway down the abdomen with 25 conspicuous longitudinal folds. The proximal part of the posterior abdomen does not contain gonads but this region is often contracted. The ovary is present just anterior to the double row of testis follicles that occupy the greater part of the posterior abdomen. The heart is a wide U-shaped tube in the distal tip of the posterior abdomen.

***Pseudodistoma cereum* Michaelsen, Kott, 1972a: 12 (synonymy); 1972b: 173.**

New Record: Margaret Brock Reef (Cape Jaffa).

Remarks: Specimens in the present collection measure up to 12 cm of which the pointed or rounded head represents half of the total length. The zooids, opening all around the head, are small, the contracted thorax and abdomen together measuring only 2 mm. (Kott 1972a, 2 cm *sic*.)

Subfamily POLYCLININAE

***Polyclinum neptunium* Hartmeyer, Kott, 1972b: 175 (synonymy).**

New Record: Investigator Strait (Sta Y11).

Description: The present colonies are small, with rounded heads only about 3 mm in diameter on thin, branching stalks. Each head contains about 6 zooids surrounding a central common cloacal opening. The test is very delicate. There is no sand internally but externally there is a heavy encrustation.

The zooids are minute. The atrial lip is typical of the genus (Kott 1963) and has 4 longitudinal muscle bands. It arises from above the upper rim of the opening and appears to close down over the aperture which is produced to point directly anteriorly. There are 7 muscle bands radiating from the branchial aperture but these do not extend onto the posterior part of the thorax. There are 5-8 small oval stigmata in each of the 7 rows, and papillae on the transverse vessels coincide with the stigmata. The gonads are not developed. The stomach is smooth.

Remarks: Although the number of muscle bands in the atrial lip, and the number of rows of stigmata and the number in each row, are very much less than that usually reported for this species, the arrangement of the branchial papillae is the same as that usually reported (Kott 1972b), and it is possible that the colonies are juveniles.

***Aplidium foliorum* n. sp.**

Type Location: northern Great Australian Bight (32°24'S, 133°30'E), 42 m deep, P. Symond, 5.v.1973. **Holotype:** SAM, E 1036.

FIGS 4-6

Description: The colony is a circular cushion 6 cm in diameter and 2 cm high, forming a low dome, slightly concave basally where the zooid bearing surface layer of the test on one side has grown around onto the basal surface to form a crescent shaped pocket invaginated towards the border of the colony where the surface zooid bearing layer of test has grown to overlap it. The test is soft, gelatinous and semi-transparent. There are about 8 common cloacal apertures scattered over the surface of the colony, about 1.5 to 2 cm apart. Canals radiate out from the openings, lined on each side by rows of zooids. These radiating canals subdivide many times and zooids lining them on each side crowd the test. Zooids are at right angles to the upper surface.

The branchial aperture is terminal with the opening surrounded by a circular sphincter. The atrial lip rising from the upper border of the aperture is very variable and may be simple or tripartite, while the lobes may be large and foliate or small and pointed. There is a band of muscles down the centre of each atrial lobe. There are 14 rows of about 15 stigmata. The stomach is large with 18 to 25 narrow longitudinal folds.

The zooids are long and thread-like, the posterior abdomen comprising the great part of their length while the thorax and abdomen together are only 2 mm long. There are one or two embryos at very different stages of development in a brood pouch that is formed by an expansion of the distal end of the oviduct at the postero-dorsal end of the thorax. Dense testis follicles are present in two rows in the posterior abdomen. The ovary is present anterior to the testis (in the usual position for this genus).

Larvae: The larvae are 0.75 mm long with a long tail that completely encircles the body. There are the usual three anterior papillae

alternating with two median ampullae. Numerous ampullary vesicles rise from the lateral ridges extending anteriorly along both sides of the endostyle and to the post ventral aspect of the larval body.

Remarks: The species is distinguished from *Aplidium pliciferum* by the larger size of the colony, the very distinct radiating double rows of zooids which comprise the systems, and by the characteristic foliaceous muscular atrial lobes that are present on many of the zooids. The colony does resemble that of *A. australiensis* which has similar systems and in which the branchial sac is the same. In *A. australiensis*, however, there is a lesser number of stomach folds and they are sometimes irregular and oblique, while the zooids lack the distinctive atrial lobes of the present species. The larvae of *A. pliciferum*, *A. australiensis* and the present species are, however, identical. There are slight variations in size (e.g. larvae from the holotype of *A. australiensis* are 0.9 mm long) and in the length of the tail which extends from half to the entire distance around the body. However, the relationship of the length of the tail to the larval body does not appear to be constant for any single species. The characteristic atrial lobes of the present form are similar to those described for *A. elatum* Kott, 1972b, which however differs considerably from the present specimen in colony form.

***Aplidium flavolineatum* (Sluiter) Kott, 1972b: 176 (synonymy).**

New Record: northern Great Australian Bight.

Description: The colony is mushroom shaped, 4 cm in diameter across the flat upper surface and 2 cm high. The flattened zooid-bearing head narrows very suddenly to a short stalk from the centre of the under surface. Sand is present on the stalk and, to a lesser extent, on the upper surface. The test is clear and glassy but soft. The zooids are crowded in the test and it was not possible to distinguish the form of the systems. Zooids open only onto the upper surface. They are 6 mm long, of which the thorax is 2 mm and abdomen only 1 mm. The posterior abdomina cross one another in the internal test although the thoraces are parallel at the surface. The atrial lip is divided into 3 very pointed lobes from the upper border of the opening. There are 12 fine longitudinal muscles on the thorax. There are 12 rows of 10 long rectangular stigmata. The stomach is

especially small with 17 distinct longitudinal folds. There are 2 rows of testis follicles in the posterior abdomen.

Larvae: Up to 5 developing embryos are present in the atrial cavity. They are 0.75 mm long, have 3 median papillae alternating with single median ampullae and corresponding lateral ampullae develop from the lateral ridge. The median ampullae are narrow and in some cases appear to be bifurcated. There are also clusters of ampullary vesicles both above the endostyle and ventral to the body of the larva. The tail winds about three quarters of the way around the body of the larva.

Remarks: The colony and zooids are of similar form to those described previously for *A. flavolineatum* with the exception of the stomach in which there are only 17 folds. The size and shape of the stomach and the course of the longitudinal folds are similar to those described previously for this species.

***Aplidium coniferum* Kott, 1963: 102.**

New Records: Elliston Reef. **Previous Records:** N.S.W. (near Twofold Bay, 10–70 m deep; Montague North, 13 m deep)—Kott 1963.

Description: Sessile, rounded lobes about 4 cm in greatest diameter. The test is sandy internally, but the external layer of test is free of sand and is smooth and gelatinous. Zooids are long and narrow and open all around the head. There is a small pointed atrial lip from the body wall anterior to a muscular siphon that is present about one third of the distance down the dorsal surface. The thorax is long and narrow with about 15 rows of 10 stigmata. There are 5 stomach folds.

Remarks: The specimen agrees with those previously described. The clear external layer of test without sand and the form of the colony are apparently characteristic of the species.

***Aplidium amorphatum* Kott, 1963: 101.**

New Record: Elliston Bay. **Previous Record:** Vic. (38°51'S, 146°55'E)—Kott 1963.

Description: The colony is soft, sessile and dome shaped. The test is semi-transparent, without sand. Zooids open all around the upper surface and no systems are evident. The zooids are very small and irregularly oriented in the test so that they cross one another. There are 10 longitudinal thoracic muscles. The atrial aperture is on a short siphon. The upper rim of the aperture is produced into a pointed lip.

There are 12 rows of about 10 stigmata. Each row is crossed by a parastigmatic vessel. The stomach is small with 5 folds.

Larvae: The atrial cavity is occupied by a single large embryo, 1 mm long. It has the usual 3 median, stalked, papillae and numerous ampullary vesicles are developed from the anterior part of the body.

Remarks: The specimen is identical with that previously described for the species. The larva is the same as that of *A. pantherinum* (see Kott 1963). The shape and consistency of the colony differ, however, and resemble *A. protectans* (Herdman); Kott 1963. In the latter species, however, the zooids are larger, the branchial sac larger, there are more thoracic muscle bands and the parastigmatic vessels are not present.

***Aplidium prorum* n. sp.**

Type Location: Investigator Strait (Stn X1), 9 m deep, Watson, Jan. 1971. **Holotype:** NMV. H 287.

FIG. 7

Description: The colony consists of small, flat-topped lobes united basally. The test is soft and there is very little sand internally. There is a single common cloacal aperture in the centre of each lobe. The zooids are more than 1 cm long and thread-like. The thorax and abdomen are of equal length, and about one third of the total length of the zooid. The atrial lip is bifid or trifid terminally and extends from the upper border of the atrial opening which is on a short siphon. There are 11 rows of 12 stigmata and 8 very weak stomach folds. There are 20 longitudinal thoracic muscles.

Remarks: The colonies resemble those of *A. novaezealandiae* Brewin and *A. cottrelli* (Brewin) from New Zealand, although the flat-topped lobes. Brewin (1952, 1957 respectively) described for both these species have several systems, only 5 stomach folds, and the atrial siphon is not produced. The atrial siphon of *A. maritimum* (Brewin, 1958a) is, in fact, produced in the same way as in the present species, and the stomach has the same ill-defined folds. However, the longitudinal thoracic muscles are more plentiful in the present specimens, there are fewer stigmata in each row, the posterior abdomen is longer and more thread-like, and there is only a single system in each lobe. Further, in Brewin's species the lobes are separate and do not appear to be con-

tinuous in their basal half as in the present species.

***Aplidium digitatum* n. sp.**

Type Location: northern Great Australian Bight (32°24'S, 133°30'E), 49 m deep, 5.v.1973, P. Symond. *Holotype:* SAM, E 1030. *Paratypes:* QM, G 7508; AM, Y 1982.

FIG. 8

Description: The colonies are long, branched, cylindrical stalks 2–3 cm long, terminally rounded and slightly expanded to overlap the stalk. The zooids open onto these terminal expansions. Sand is absent only from the surface test where the zooids open on the expanded terminal portion of the lobes. The stalk is densely encrusted with sand. The test is firm, especially in the stalk, and is impregnated with sand throughout. Zooids are minute, but long and thread-like, crowded in the test and extending parallel to one another down the stalk. There are 15 rows of about 8 stigmata. There is a long, pointed, atrial lip from the upper border of the opening. The stomach has 12 longitudinal folds. There is a double row of testis follicles in the long posterior abdomen. There is a large common cloacal opening in the centre of each lobe.

Remarks: The colonies resemble those of the Antarctic species *Aplidium recumbens* Kott, 1969, but are distinguished by the large number of distinct longitudinal folds in the stomach. The zooids are especially delicate and narrow.

***Aplidium colelloides* (Herdman). Kott, 1972b: 176 (synonymy).**

New Record: northern Great Australian Bight.

Family DIDEMNIDAE

***Polysyncrator aspiculatum* Tokioka, 1949: 2. Kott, 1962: 301.**

Polysyncrator magnilarvum Millar, 1961: 13 (*nomen nudum*); 1962: 165. Kott, 1972b: 178.

New Records: northern Great Australian Bight; Investigator Strait. *Previous Records:* W. Aust. (Rottneil I., Pt Peron)—Kott 1962. S. Aust. (Investigator Strait)—Kott 1972b. Qld (Mackay)—Kott 1962. S. Africa—Millar 1962. Mozambique—Millar 1961. Japan—Tokioka 1949.

Description: The colony from the Great Australian Bight is a soft jelly-like cushion. The

common cloacal system consists of narrow canals at oesophageal level, radiating from common cloacal apertures and lined on either side by zooids. There are no spicules. The zooids are of moderate size, with 4 rows of stigmata and a long bifurcated atrial tongue. The oesophageal neck is long. Gonads are not mature.

The colony from Investigator Strait (that is doubtfully assigned to this species) consists of 2 large flattened lobes rising from a fleshy cylindrical common basal stalk. The zooids are embedded in the surface layer of test. The common cloacal canals extend between clumps of zooids beneath an especially thin layer of surface test. There are very extensive cloacal spaces between the central, soft test that forms the central core of each lobe and the surface that is only occasionally joined with the central core by solid test connectives. Secondary canals extend between the zooids beneath a very thin layer of surface test. The test is colourless and transparent, and the zooids show through it as white dots. There are no spicules. Zooids have a long oesophageal neck, and the usual 4 rows of stigmata. Gonads are not mature in this colony.

Remarks: Specimens assigned to both *P. aspiculatum* Tokioka, 1949 and *P. magnilarvum* Millar, 1962, are soft and rounded, stalked or sessile, from 3 to 7 mm thick, with variable spicule distribution to an aspicular condition. The atrial lip is long, and often spread or bifurcate at its tip. There are also, in both, a large number of testis follicles (8–12) and large larvae (over 1 mm long) with up to 15 pairs of lateral, finger-like ampullae and precocious buds. Zooids of both species are also characterised by a long oesophageal neck. In Australian specimens the ventral surfaces are embedded in the common test and they are arranged along both sides of common cloacal canals that demarcate rounded zooid-free swellings of the surface of the colony. In neither species has the common cloaca been described as posterior-abdominal. The shape of the present colony from Investigator Strait is identical with others from this area that are assigned to *P. aspiculatum* (>*P. magnilarvum*; Kott 1972b). The posterior abdominal cavities in this colony, however, do not occur in those previously described. Positive identification is not possible owing to the lack of mature gonads, and the relationship of the extensive cloacal system with the simple canals that have been

previously described is not known. The cloacal system is the same as that of *Didemnum tum- bitum* and *Polysyncraton chondrilla* but both these species have only a single aperture and are not known without spicules.

***Leptoclinides volvus* n. sp.**

Type Location: northern Great Australian Bight (32°24'S, 133°30'E), 42 m deep. *P. Symond*. *Holotype:* SAM, E 1034. *Para- types:* SAM, E 1033; QM, G 7511.

FIGS 9, 10

Description: The specimen designated as the holotype is a flattened sphere 5.0 cm in diameter and 3 cm thick, with a thick but very short stalk, constricted to 2 cm in diameter where it joins the body. The paratypes are entirely spherical, about 3 cm in diameter, and are without stalks although the base of the colony is identified by the absence of zooids and by foreign matter that is included in the test material which has overgrown the area. There is a single, apical, sessile, and inconspicuous common cloacal aperture, opposite the base of the colony at the junction of several common cloacal canals. Zooids are arranged along both sides of narrow cloacal canals at the abdominal level of the zooids and the surface of the colony is depressed above these canals. These depressions demarcate rounded swellings of the surface of the test corresponding to zooid-free areas. The test is very firm gelatinous and translucent. There is a layer of bladder cells superficially. A sparse layer of spicules is present in the zooid layer of test and these are most dense around the zooids, thus indicating their position through the test. The spicules are minute, 0.015 to 0.02 mm in diameter, some stellate and others with needle-like rays. There are minute, spherical, brown, pigment cells scattered throughout the test. Zooids are small, with about 8 stigmata per row. The branchial siphon is of moderate length. The atrial siphon is very short, rising from the mid dorsum, opposite the space between the second and third rows of stigmata. It is surrounded by a circular sphincter muscle and is posteriorly or laterally directed. There are 5½ coils of the vas deferens and up to 10 testis follicles. Large ova are present in the test at abdominal level but none of these appear to be developing embryos.

Remarks: The spherical body, constricted stalk and single common cloacal opening are unusual in this genus. The lack of stalk in the two para-

types, together with the spherical shape, suggest that these colonies may be free living, although the foreign particles that are embedded in the basal region suggests that this part of the colony was fixed to the substrate, broke free and was overgrown by the surface test. The constriction where the broadening stalk joins the head in the holotype also supports the suggestion that the spherical head may break away. Certainly the configuration of the surface, with the projecting swellings of solid gelatinous test, while the zooids, their openings, and the common cloacal aperture are depressed into the surface of the test, would all accommodate a free living habit in which the colony is able to roll over the sea floor as in some coral species (see Glynn 1974, Pichon 1974).

The limited nature of the common cloacal system is unusual in this genus where extensive posterior abdominal spaces are usually developed. It differs from species in other genera, in which the zooids are arranged along both sides of narrow common cloacal canals that extend around circular zooid-free areas, in that the canals are at the abdominal rather than the thoracic level (see *Polysyncraton aspiculatum*, above; and *Didemnum patulum*, Kott 1972a).

Stalked species are also unusual in this genus, *L. fungiformis* Kott, 1972b being the other that is known. It is distinguished from the present species by its undivided testis follicle.

***Leptoclinides reticulatus* (Shuiter). Kott, 1962: 285 (synonymy); 1972a: 18; 1972b: 180.**

New Record: northern Great Australian Bight.

Description: A large colony, investing a specimen of *Herdmania momus*. There are streaks of orange-brown, stellate, pigment cells scattered amongst the spicules in the surface test. The spicules have 7 rays in optical transverse section and are 0.03 to 0.05 mm in diameter. There is a superficial layer of bladder cells mixed with spicules. Spicules are dense at the zooid level but are absent basally, below abdominal level. Common cloacal canals were not found and the thoraces of the zooids appeared to be partially disintegrated although the abdomina were in good condition with 5½ coils of the vas deferens around 5 to 9 testis follicles. Small vegetative buds are present in the oesophageal region.

Remarks: The absence of common cloacal canals and the condition of the zooids suggests that the colonies may present a quiescent winter

condition. The presence of vegetative buds and mature gonads suggests the onset rather than the end of this quiescent phase.

Leptoclinides rufus (Sluiter): Kott, 1962: 286 (synonymy); Eldredge, 1967: 221.

Leptoclinides lissus: Millar, 1963: 704.

New Records: Elliston Bay (outside bar, and 25 m deep). *Previous Records*: S. Aust. (Port Noarlunga). Tas. (Marla I.). Vic. (Shoreham)—Kott 1962. N.S.W. (Port Jackson)—Kott 1962, Millar 1963. Qld (Bargara, Hefun I., Low Isles)—Hastings 1931; Kott 1962. Indonesia (Paternoster I., Arafura Sea)—Sluiter 1909, 1913; Tokioka 1952, New Zealand (North Island)—Michaelsen 1924; Brewin 1958b; Millar 1960. Hawaii (Oahu)—Eldredge 1967.

Description: Living colonies are reddish brown or grey with orange around the siphons. They are firm and investing, with common cloacal openings in the centre of evenly spaced rounded swellings. The common cloacal apertures are about 1 cm distant from one another. There is a surface layer of bladder cells and spicules are especially dense below this layer. They gradually become less dense and are absent altogether from the basal half of the colony. Although they are present in a layer at the base of the common cloacal cavity, they are stellate, 0.02 to 0.04 mm in diameter with pointed conical rays. The spicules are especially densely accumulated around lobes of the branchial apertures.

The common cloacal cavity is posterior abdominal, extending into circular chambers beneath the common cloacal apertures.

The zooids are about 2 mm long with up to 12 longitudinal thoracic muscle bands from which fibres branch and anastomose with adjacent bands. There is a minute circular lateral organ opposite the 4th row of stigmata. The atrial aperture is directed posteriorly as is usual for the genus. There are up to 10 stigmata in each row. The oesophagus is long. The gut loop may be curved, although it also occurs as a long straight loop. The gut is clearly differentiated into duodenal and mid intestinal regions and a posterior stomach swelling. The stomach is smooth and rounded, longer than its diameter. There are 9 to 10 testis follicles and $7\frac{1}{2}$ coils of the vas deferens.

Remarks: The synonymy of *L. lissus* Hastings, from Low Isles, with *L. rufus* originally described from Indonesia and the Arafura Sea to

the north, within the same biogeographical region, was arrived at after comparison of Hastings type material (AM. G 13449) with other specimens from a wide range along the southern and eastern Australian coast, including the Great Barrier Reef and the Queensland mainland. The type specimen of *L. diemenensis* has not been examined, although Tokioka (1952), Millar (1960), and Kott (1962) have not been able to identify any character that could distinguish the two species. Its synonymy with *L. rufus* is here maintained. The range of *L. rufus* is, therefore, similar to that of many wide ranging species of this family in both tropical waters (Kott 1974) and in Antarctic waters (Kott 1969a). The other related New Zealand species, *L. sluiteri*, *L. auranticus* and *L. novae-zelandiae*, are distinguished only by the larger number of coils of vas deferens, the relatively shorter oesophagus and the smaller zooids. Further specimens are needed to adequately determine the parameters of each of these species. *L. rufus* is characterised by its relatively large zooids with distinct longitudinal thoracic musculature but no retractor muscle; by its long oesophagus and gut loop and the clearly demarcated gut regions; by its long and muscular siphons; by the invasion of spicules into the superficial bladder cell layer and by the position of the small lateral organ in the posterior part of the thorax. The number of testis lobes in the present specimens is greater than the maximum of 7 previously recorded.

Didemnum candidum Savigny, Kott, 1972a: 19 (synonymy); 1972b: 179.

New Record: northern Great Australian Bight.

Didemnum moseleyi (Herdman), Kott, 1972a: 19 (synonymy); 1972b: 179.

New Record: northern Great Australian Bight.

Trididemnum savignii (Herdman) s. sp. *savignii* Herdman, Kott, 1966: 285 (synonymy); Eldredge 1967: 179.

New Record: Sellick Beach (south of Adelaide), S. Aust.

Description: Extensive investing colony with round, smooth, margins. There is a spicule-free surface layer of bladder cells. Spicules are sparse in the zooid layer and are absent altogether from the basal half of the colony. The common cloacal canals are deep, extending the whole length of the zooids, but they are not

posterior abdominal. The spicules are 0.04–0.08 mm in diameter. They are stellate with 12 conical rays in optical transverse section. The zooids are surrounded by black pigment particles that are often but not always accumulated into the usual pigment patch at the anterior end of the endostyle. There is a distinct atrial siphon which is laterally rather than posteriorly directed in these colonies. There is a distinct retractor muscle. The testis is not mature and the vas deferens was not distinguished.

Remarks: No further evidence is available from the examination of these specimens that could clarify the relationship between this Indo-Pacific subspecies and the Atlantic Ocean form *T. savignii* subsp. *atrocolum* Van Name (see Kott 1966). It should be noted that the Pacific Ocean specimens (Eldredge 1967) have the 7–8 coils of the vas deferens that is associated with the Indo-Pacific form (Kott 1966).

Trididemnum cerebriforme Hartmeyer. Kott, 1972c: 47 (synonymy).

Trididemnum savignii; Tokioka, 1967: 80; var. *johense*: 82.

New Record: Sellick Beach (south of Adelaide), S Aust.

Description: The colonies are investing and of variable thickness. Conspicuous common cloacal apertures with frilled lips are distributed randomly over the surface of the colony. Posterior abdominal cloacal canals radiate from these apertures. Spicules are sparse in the upper layer of test and apart from a layer lining the test along the floor of the common cloacal cavity, they are entirely absent from the basal layer of test. The spicules are stellate, 0.02 to 0.04 mm in diameter, with about 6 rays in optical transverse section.

The body wall of the thorax is covered with black pigment particles although these are absent from the abdomen. The pigment particles are accumulated in a patch over the anterior end of the endostyle. The atrial siphon is posteriorly directed. There are 6½ coils of the vas deferens around an undivided testis follicle.

Remarks: The relationship of this species to *T. savignii* is perplexing since its three-dimensional common cloacal system provides the principal distinction. *T. cerebriforme* acquires great complexity in its common cloacal system with growth, but juvenile colonies must necessarily display a cloacal system identical with that of *T. savignii* before its subsequent proliferation,

as the colony thickens and surface folds develop. In the present specimens, both taken from Sellick Beach, each species has spicules of different sizes although this size difference was not observed in specimens previously described. The number of spicule rays as previously reported, however, is greater for *T. savignii* than for *T. cerebriforme*.

Diplosoma translucidum (Hartmeyer)

Leptoclinum (*Leptoclinum*) *translucidum*; Kott, 1962: 306 (synonymy).

New Record: Investigator Strait (Sta X1).

Previous Records: Indonesia—Sluiter 1909. North Western Australia—Hartmeyer 1919. W. Aust. (Oyster Harbour, Albany)—Kott 1962.

Description: The colony is irregularly lobed, investing weed or other ascidians. Each lobe is flattened, about 2 cm wide, 0.5 cm thick and up to 3 cm long. One colony completely envelops a specimen of *Pyura australis* in which only the apertures are exposed. The surface is smooth, and the zooids show through as white dots. They are small and crowded at the surface of the colony in groups of about 8.

There is a large ovum present in most zooids but the testis is not mature and no coils of the vas deferens were detected.

Remarks: The tough, firm transparent test and the extensive cloacal system is characteristic of this species.

Family ASCIDIIDAE

Ascidia thompsoni Kott; 1972a: 27 (synonymy); 1972b: 181.

New Records: upper Spencer Gulf.

Description: Specimens have a gelatinous test, sometimes thick and furrowed. Both apertures are present on siphons, usually both directed dorsally or anteriorly and sometimes very long. The animal is fixed ventrally and by most of the left side. There is sometimes a coating of sand encrusting the body, but sand is never present on the siphons. The body wall has the usual meshwork of muscles on the right side of the body. The anterior part of the dorsal lamina is a double membrane, ribbed on the outer sides but not in the centre. The ribs of the dorsal lamina extend into pointed projections on the free edge of the membrane.

The neural ganglion is about one-third of the body length from the dorsal tubercle.

Remarks: The specimens from Station D3 on the floor of the channel are encrusted with a

layer of sand absent only from the siphons which project upward from the middle of the upper surface. In this specimen, the right side of the body is narrower than the left and comprises the right side of the upper surface, while the base, by which the animal is fixed, is the ventral surface and a large part of the left side of the body. In specimens from G4, also on the floor of the channel, the siphons are especially long, both directed upwards, and the right side of the body is similarly short.

The very long external siphons directed upwards, and the sand encrustation, are unusual in this species. *Aeidia aelara* is the only species of the genus in which a similar sand encrustation hardens the test. The long, cylindrical extensions of the test that, in *A. aelara*, create a canal or tube from the sessile apertures extending upwards from the animal, are analogues rather than the homologues of the long siphons in the present forms. It is also of interest that, in specimens from stations D3 and K4, where the siphons extend dorsally, their central position, from the middle of the upper surface of the body, is achieved by relative narrowing (i.e. between the dorsal lamina and the endostyle) of the right side of the body; whereas in *A. aelara* it is the left side of the body that is narrower than the right. The base of the present specimens is the ventral and two-thirds of the left surfaces of the body, while in *A. aelara* it is two-thirds of the right side, between the dorsal lamina and endostyle (Kott 1972d).

The specimens appear to have adapted to their free existence on a shifting sandy sea floor by these morphological variations in the position and length of the siphons.

Ascidia aelara Kott, 1972d: 236 (synonymy).

New Record: Goat I. (off Ceduna).

Family STYELIDAE

Stolonica carnosa Millar, 1963: 734. Kott, 1972a: 28.

New Record: Investigator Strait (Stn Y1).

Remarks: The present specimens are small and sandy individuals joined by stolons. There are only 3 stigmata per mesh and the longitudinal vessels in the branchial sac are slightly fewer than previously reported, viz. DL0(5)2(4)1E. It is probable that this is a young colony, which is characterised by a pyriform stomach with narrow folds and a long curved caecum that extends into the gut loop from the suture along the lateral aspect of the stomach.

Amphicarpa diptycha (Hartmeyer). Kott, 1972c (synonymy).

New Record: northern Great Australian Bight.

Oculinaria australis Gray. Kott, 1972a: 29 (synonymy); Kott, 1972b: 184.

New Record: Elliston Bay.

Symplegma viride Herdman. Kott, 1952: 252 (synonymy); 1962: 129. Millar, 1966: 368. Plante & Vasseur, 1966: 149. Tokioka, 1967: 162 (synonymy). Vasseur, 1967: 111.

New Record: Elliston Reef.

Subfamily BOTRYLLINAE

PARABOTRYLLUS n. gen.

Colonies are elongate branching stalks slightly expanded terminally. One to 3 circular systems of zooids are present in each terminal expansion, opening onto a more or less flattened surface of each free lobe. Each system of zooids surrounds a central common cloacal aperture. The terminal ampullae and conspicuous blood vascular system that are present in other genera of this subfamily are absent. The rim of the branchial aperture is smooth. The atrial aperture has a single anterior lip. There are only 2 internal longitudinal vessels in the branchial sac. Eggs are endogenous.

Remarks: The zooids are not conspicuously different from those of the genera *Botryllus* and *Botrylloides* except in the presence of only 2 internal longitudinal vessels in the branchial sac. The colony differs considerably, however, both in its shape, and in the presence of only one to three systems opening onto the flat terminal surface of each lobe. Buds are present in the common test near the posterior region of the adult zooids, to which they are joined by narrow connectives from the oesophageal region of the parent. The buds in this genus therefore do not, apparently, maintain a close connection with the parent until a late stage in their development as they do in other genera of the sub-family. The zooids are endogenous and have three to four developing ova on each side as in *Botryllus*, while *Botrylloides* produce only single ova on each side of the body.

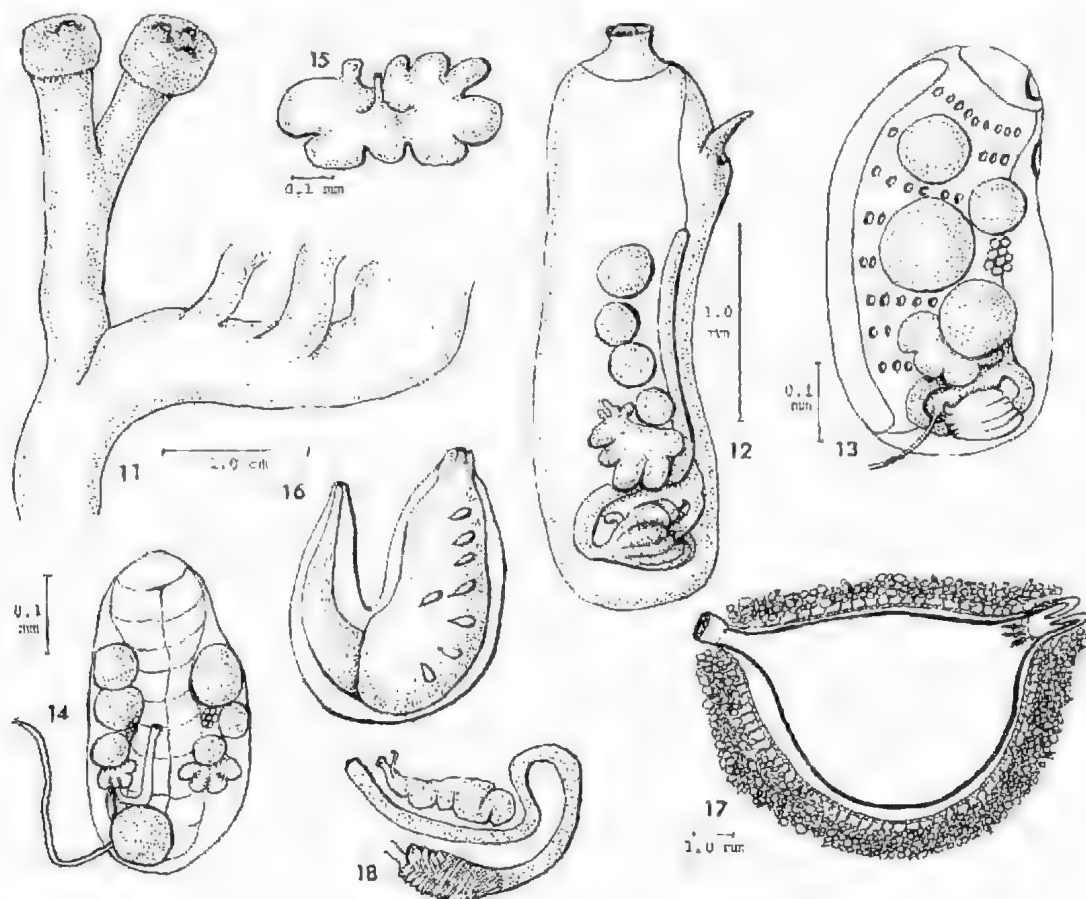
Parabotryllus nemorus n. sp.

Type Location: upper Spencer Gulf (Stn G), 9 m deep, floor of channel. S.jx.1973. *Holotype:* SAM, E 1031. *Paratypes:* AM, Y 1981; QM, G 7507.

FIGS 11-15

Description: The colonies consist of narrow, sandy lobes, 1-1.5 cm long, usually branched. The superficial layer of test is encrusted with sand but is neither stiff nor brittle. Internally sand is absent and the test is very soft. There are circular systems of zooids opening onto the upper free end of the lobes surrounding the central common cloacal apertures that are slightly depressed into the surface. Generally there is only a single system in each terminal branch of the colony although occasionally there are 1 or 2 smaller additional systems. The blood vessels in the test are short and relatively few for this subfamily. They terminate in elongate rounded bulbs at the base of the zooids. The zooids are about 2 mm long. The rim of the branchial aperture is smooth and the atrial

aperture, in the anterior third of the dorsal surface, has its upper lip produced into a single pointed lip. The atrial aperture is very small and is directed anteriorly so that the upper lip closes over it (as in *Polyclinum*). There are 10 rows of stigmata with about 10 stigmata in each row and two internal longitudinal vessels on each side of the body. The gut forms a single tight loop on the left side of the branchial sac. The stomach is pyriform with about 8 distinct longitudinal folds and there is a short curved caecum, of moderate length and expanded into a terminal bulb, from the pyloric end of the stomach. There is a connective extending from the pyloric region of the stomach to the intestine. There is a single, flat, testis follicle with lobed margins on each side of the branchial sac just anterior to the gut loop.



Figs 11-15. *Parabotryllus nemorus*. Fig. 11.—Portion of colony showing branching stalks. Fig. 12.—Adult zooid. Fig. 13.—Bud (lateral aspect) showing connecting vessel. Fig. 14.—Bud (dorsal aspect) showing endogenous ova. Fig. 15.—Testis.
 Fig. 16. *Polycarpa tinctor*. Aberrant individual with atrial siphon produced anteriorly.
 Fig. 17. *Pyura tendata*. Section through the body wall, test and sandy coating.
 Fig. 18. *Microcosmus planus*. Gut and gonad on left side of the body.

The vas deferens, arising from the middle of the mesial surface of the testis, is very short. There are three or four ova in the body wall anterior to the testis lobe. These are endogenous and project into the peribranchial cavity. Developing buds are present in the test on either side of the posterior end of the adult zooids. These contain four large ova on each side of the body and a clump of large cells dorsal to the ova. It is possible that these may be precociously differentiating buds. The buds at this stage of development are 0.25–0.5 mm long. There is a blood vessel extending from the posterior end of each bud in the region of the oesophagus.

Remarks: The species is distinguished from others in the subfamily by the large number of ova and internal longitudinal branchial vessels, the relatively limited blood vascular system in the test, and the form of the colony and the limited development of colonial systems. The internal test is also very soft in comparison with that of other species in the subfamily. The buds appear to undergo the major part of their development in the test in connection with the colonial blood vascular system and in the present colonies there were no buds found directly associated with the parent zooids. The testis of this species is reminiscent of that in *Symplesma*, while the multiplicity of ova resemble *Rotellus* and the endogenous nature of their development and the small circular systems in the colony are also reminiscent of the latter genus.

Subfamily STYLLINAE

Polycarpa tinctor (Quoy & Gaimard). Kott, 1964: 134 (synonymy); 1972b: 186; 1972c: 254; 1972d: 242.

New Record: upper Spencer Gulf (Stn B10).

FIG. 16

Remarks: One of the specimens is highly modified. It has the usual short branchial siphon from the anterior end of the body. The atrial siphon, however, extends anteriorly from the posterior half of the dorsal surface parallel with the anterior half of the body and opens at a point more or less level with the branchial aperture, so that the individual is U-shaped. The lower half of the body is encrusted with large particles of sand but the upper half has only fine sand encrusting it, and it appears that the animal had been half buried in the floor of the channel and that the atrial siphon was pro-

duced upwards so that it opened above the sea floor. In another specimen there are long root-like processes from the ventral border of the body, which is otherwise typical of the species (Fig. 16). In the U-shaped specimen there is a single row (17) of long polycarps around the ventral border of the body and only occasional polycarps, representing a second row, scattered dorsal to these.

Polycarpa pedunculata (Heller). Kott, 1972a: 35 (synonymy); 1972b: 186.

New Records: upper Spencer Gulf; northern Great Australian Bight; Investigator Strait. For Previous Records, Description, see Kott 1972a, 1972b.

Remarks: From the upper part of Spencer Gulf, arenaceous and naked specimens are taken, sometimes growing side by side attached to the same shell or stone. There are a large number of specimens and they are either stalked or sessile. Naked specimens with a leathery test were a bright yellow colour in life but pinkish in preservative. Living arenaceous specimens were a sandy colour with a reddish tinge. There are small, smooth, black individuals in the preserved material and some that are larger with rough leathery and rather thin test. In nature such specimens with a smooth test are bright yellow (S. A. Shepherd, pers. comm.).

Polycarpa papillata (Sluiter). Kott, 1972a: 34 (synonymy).

New Record: upper Spencer Gulf (Stn B7).

Remarks: 2 specimens only are available. One is juvenile with a whitish coloured test and without developed polycarps. The other mature individual has a row of eight long polycarps around the ventral aspect of the left body wall, with the ducts directed towards the atrial opening. There are five rounded anal lobes slightly bifurcated and only two polycarps are present in the middle of the right body wall. The specimen otherwise conforms with previous descriptions of this species.

Styela pedata (Herdman). Kott, 1972b: 185 (synonymy).

New Records: northern Great Australian Bight.

Styela plicata (Leseuer). Kott, 1972b: 185; 1972c: 254; 1972d: 239 (synonymy). Tokloka, 1967. Abbott & Johnson, 1972: 95.

New Record: Port River (St Vincent Gulf).

Remarks: The individuals are small and the rounded swellings of the test are obscured by epiphytic growth. However, the species is readily distinguished by the short vasa efferentia, branched testis follicles, undulating (sometimes branched) ovarian tubes, long oesophagus, long rectum, deep secondary gut loop, long voluminous stomach with internal folds and the small leaf-like endocarps that cover the body wall and the gut loop distal to the stomach.

The gut loop is reminiscent of that of *S. ramificata* (Kott 1972d) although the rectum and oesophagus are longer in the present species; and although the gonads resemble those of *S. partita* (Stimpson), in the present species the oesophagus is shorter and the vasa efferentia are shorter (Vasseur 1967).

Cnemidocarpa etheridgii (Herdman). Kott, 1972a: 31 (synonymy); 1972c: 253.

New Record: northern Great Australian Bight.

Family PYURIDAE

Pyura tendata Kott, 1972b: 186.

New Record: south of Goat Is. (off Ceduna).

FIG. 17

Description: A single specimen only is available. It is more or less a half circle in outline, one cm in diameter. The external siphons extend from the anterior and posterior ends of the more or less straight dorsal surface. The branchial aperture is directed anterodorsally and the atrial aperture is directed posterodorsally. The external test is covered by a thick coating of sand held in place by hair-like extensions from the test. There is a thin space between the sandy coating and the surface of the test, traversed only by the base of the test hairs. There is also a coating of very fine sand on the surface of the test itself. The apertures are lined with a very tough invagination of the test. The branchial siphon is especially muscular and appears to be eversible. The body wall is also very muscular. The atrial siphon is muscular but not eversible and its aperture is protected by a well developed velum at the distal end of the siphon. Beyond this velum the test is produced into a cylindrical fibrous extension for a short distance. There are seven branchial folds on each side of the body with 14 strong internal longitudinal vessels very closely placed on each fold. There are no internal longitudinal vessels in the interspace

between folds. The branchial tentacles are of varying sizes and twice pinnate. The dorsal lamina is produced in a series of pointed languets. The gut forms a narrow straight loop and there is a mass of branched liver tubules in the gastric area. Gonads are divided into separate paired polycarp-like sacs extending along both sides of the central common duct.

Remarks: This specimen agrees in most aspects with those described from Investigator Strait, although the sandy coating is not as thick in the present specimen. Nevertheless, the nature and orientation of the siphons are identical as are the internal organs, viz. the branchial sac, the gut and the gonads. The atrial velum in the specimen from Investigator Strait was present at the base of the atrial siphon rather than more terminally as in the present specimens, and this is possibly related to thickness of the sandy coating. The test beyond the velum is apparently produced to accommodate the thickness of the sand surrounding the animal.

Pyura pachydermatina (Herdman) s. sp. **gibbosa** (Heller). Kott, 1972b: 187.

Cynthia gibbosa (Heller), 1878: 27.

Pyura gibbosa; Michaelsen & Hartmeyer, 1928: 410. Non *P. pachydermatina* var. *gibbosa*; Kott, 1952: 265 (<*P. pachydermatina draschii*; Kott, 1972b: 187).

Pyura pachydermata var. *intermedia*; Kott, 1952: 264 (synonymy) (part). Non *P. gibbosa intermedia* Michaelsen, 1922: 391. (<*P. spinifera*; Kott, 1972b: 187).

New Record: northern Great Australian Bight. For Previous Records, Description, see Kott, 1972b (*P. pachydermatina draschii*): 1952 (*P. pachydermatina intermedia*).

Remarks: The present specimens have the typical curved spines in the branchial siphon and the anus is bordered with shallow rounded lobes.

Pyura spinifera (Quoy & Gaimard). Kott, 1972b: 186 (synonymy).

New Record: northern Great Australian Bight.

Pyura australis (Quoy & Gaimard). Kott, 1972b: 186 (synonymy).

New Record: reef, Douglas Bank. (upper Spencer Gulf).

Pyura scoresbiensis Kott, 1972a: 36; 1972b: 187.

New Record: upper Spencer Gulf (Stns F3, G).

Pyura vittata (Stimpson). Kott, 1972a: 37 (synonymy); 1972d: 243.

New Record: upper Spencer Gulf (Stn A1).

Remarks: The spines lining siphons are typically long (0.1 mm) and needle-like and overlapping. The anal border is smooth and two-lipped.

Pyura irregularis (Herdman). Kott, 1972a: 38 (synonymy); 1972b: 187.

New Record: upper Spencer Gulf (Stn B7).

Remarks: The peritubercular area has the usually blister-like appearance that is characteristic of this species. The large dorsal tubercle, however, is at the top of this area rather than, as has been previously described, at its base. The tough leathery test and strong branchial sac characteristic of this species are present.

Pyura stolonifera (Heller) s. sp. *praeputialis* Heller. Kott, 1952: 274 (synonymy); 1964: 141.

Pyura praeputialis; Millar, 1966: 372.

New Record: Outer Harbour (St Vincent Gulf). For Previous Records and Description see Kott, 1952; Millar, 1966.

Remarks: This location apparently represents the western extent of this species, which has a continuous distribution from Queensland down the eastern Australian coast. The specimens here at the apparent end of its range are smaller than have usually been recorded from other locations.

No constant difference has been detected between the South African *P. stolonifera* s. sp. *stolonifera* and the Australian *P. stolonifera* s. sp. *praeputialis* and most characters demonstrate a remarkable and overlapping range of variation in the two populations. The rounded fold of test enclosing the siphons, however, is never absent from Australian populations of this species, although it also has been reported from South Africa; occasionally projections of test surround the apertures of South African specimens but have never been observed in Australian forms. The different frequency with which these characters occur in each population suggest that subspecific rank is appropriate. This matter is discussed more fully by Kott (in press).

Halocynthia hispida (Herdman). Kott, 1968: 76 (synonymy); 1972a: 41; 1972b: 189.

New Record: upper Spencer Gulf (Stn G).

Herdmania momus (Savigny). Kott, 1972a: 41 (synonymy); 1972b: 189.

New Record: upper Spencer Gulf (Stn G); northern Great Australian Bight.

Microcosmus planus n. sp.

Type Locality: south of Goat I. (off Ceduna), 31 m deep, 17–25.xii.1967, Howlett. *Holotype:* NMV, 4284. *Paratypes:* SAM, E 1032; QM, G 7510.

FIG. 18

Description: The individuals are circular in outline and laterally flattened, with both apertures close together on the upper surface. The test is thin and completely encrusted with sand, so that the specimens resemble hardened discs of sand. The sand is maintained around the animal by hair-like extensions of the test; and posteriorly these are longer, so that a flattened sandy keel is developed which interrupts the circular outline of the body. It is apparent, therefore, that these laterally flattened individuals are embedded upright in the sand rather than lying on their side on the surface of the sea floor.

The apertures are sessile. Longitudinal muscles from both siphons radiate over the body, crossing one another in the middle of each side as is usual in this genus. There are also bands of circular muscles crossing the dorsal and ventral borders of the body. There is a conspicuous, elongate, dorsal ganglion between the two apertures. The branchial sac has 7 folds on each side of the body with six internal longitudinal vessels on each fold. Parastigmatic vessels are present. There are rectangular stigmata but no internal longitudinal vessels between the folds. The dorsal lamina is a wide, plain-edged, membrane. The gut forms the usual long, narrow, curved loop with liver lamellae in the pyloric region. The branchial tentacles are twice pinnate although the secondary branches are very short and rounded. The rectum extends anteriorly to the base of the atrial aperture, forming a deep curve with the gut loop. The anal aperture is bi-labiate. The gonads are present in the secondary gut loop and consist of a long ovarian tube often forming deep, close, curves. The ovarian tube has dense male follicles along its posterior border and on the lateral aspect of the ovarian tube against the body wall. As the curves of the ovarian tube develop, the male follicles appear to mingle with the ovary. Owing to the curving of the ovarian tube, it often appears to project back into lobes bordered by male follicles. The gonad on the right side of the body is in a corresponding position to that on the left.

Remarks: The species is unusual in the genus in that the gonads do not cross into the primary gut loop. In this respect only, it resembles *Microcosmus stolonifera*. The form of the gonads in the present specimens is, however, distinctive and the laterally flattened body is also diagnostic of the species.

Microcosmus squamiger (Michaelsen), Kott, 1972a: 43 (synonymy).

New Records: upper Spencer Gulf (Stn G); Outer Harbour (St Vincent Gulf).

Remarks: The present specimens have a thick test that is impregnated with sand, and in some cases numerous specimens form aggregates. The siphons are a rosy pinkish colour and there are the characteristic flattened scales lining the outer part of the siphons.

Microcosmus nicholsi Kott, 1972a: 42 (synonymy); 1972d: 245.

New Records: northern Great Australian Bight.

Microcosmus stolonifera Kott, 1972a: 43 (synonymy); 1972d: 245.

New Records: upper Spencer Gulf (Stn E1).

Remarks: The position of the left gonad in the secondary gut loop is characteristic of the species.

Family MOLGULIDAE

Molgula mollis (Herdman), Kott, 1952: 298; 1964: 144; 1972a: 45 (synonymy).

Molgula sabulosa, Kott, 1972d: 248.

New Records: upper Spencer Gulf (Stn B10); Investigator Strait (Stn Y1). For **Previous Records, Description**, see Kott 1972a (*Molgula sabulosa*).

Remarks: The specimens are small, more or less laterally flattened, spheres. The apertures are close together on the upper surface and a ridge of slightly thickened test extends between them. There are fine hairs on the lower part of the test which is completely encrusted with sand. The rim of the aperture is lobed but there are no hollow test expansions surrounding them as in *M. sabulosa* (see below). The apertures are directed away from one another. There are 7 branchial folds on each side of the body, with up to 9 internal longitudinal vessels on each distributed over both sides of each fold. There are no internal longitudinal vessels between the folds. The testis follicles form a complete circle at the end of the ovary, with a ligament extending through the centre of this

circle. On the lateral aspect of the ovary, it is apparent that the testis follicles embrace the end of the ovarian tube, but on the mesial aspect the U is completed to form a circle by the growth of the male follicles across the surface of the ovary. The male follicles are long and on their lateral aspect lie along the body wall directed from the periphery of the circle into the centre. On the mesial surface of the gonads, the testis follicles can be seen to be more or less fan-shaped and tightly packed with their outer border divided into separate lobes. The vas deferens extends from the centre of the circle of testis follicles and, viewed from the outside of the body, has two vasa efferentia connecting ducts from each individual testis follicle on each side. The vas deferens then extends mesially and along the surface of the ovarian tube and opens above the opening of the oviduct. The proximal part of the vas deferens is expanded into a seminal vesicle.

Remarks: The length of the oviduct and the absence of hollow test extensions around the apertures distinguish this species from the very similar *M. sabulosa* (see below) which has often been confused with it.

Molgula sabulosa (Quoy & Gaimard), 1834: 613. Michaelsen & Hartmeyer, 1928: 449 (synonymy). Kott, 1952: 298 (part); 1972b: 190. Millar, 1966: 374.

Remarks: There are no new records for this species; however, a small specimen from Elliston has made it possible to compare the species characteristics with those of *M. mollis* with which it has been confused. It is clear that the differences in the two species are not associated with maturity. *M. sabulosa* is spherical with a sandy test that is hard and brittle, while *M. mollis*, although encrusted with test, has fine hairs to which the sand adheres, the test itself is more flaccid, and the preserved specimens are laterally flattened. The branchial aperture is always protected by 6 pointed lobes from the surrounding test a little distance from the opening while the rim of the aperture itself is produced into 6 smaller pointed lobes, that are covered in the closed position by the rim of the larger lobes. The atrial aperture is protected by two flattened, wide tongues and their border is separated into three rounded lobes that arise from the test at the dorsal and ventral sides of the opening. The rim of the aperture itself is produced into 4 small,

pointed, sandy lobes and these are covered by the larger lips in the closed position. All these extensions from the test around the apertures are hollow and have prolongations of the body wall extending into them. They are characteristic of the species and are never present in *M. mollis*. The gonad in the present species, while superficially resembling that of *M. mollis*, has a very short vas deferens that opens at the proximal end of the ovary on its mesial surface.

Biogeography

The 22 species recorded from the northern part of the Great Australian Bight (including Ceduna), as far as 32°24'S, 133°30'E. can be divided into the following groups:

1. *Possibly endemic to the Great Australian Bight.*
Patridium pulvinatum n. sp.; *Aplidium digitatum* n. sp.; *Aplidium foliorum* n. sp.; *Leptoclinides volvus* n. sp.; *Paraborryllus nemorus* n. sp.; *Pyura tendata* Kott; *Microcosmus planus* n. sp.
2. *Southern temperate* (recorded also from South Africa).
Aplidium flavolineatum (Sluiter); *Aplidium coelestoides* (Herdman).
3. *Circum-australian.*
Polychor giganteum (Herdman); *Leptoclinides reticulatus* (Sluiter); *Leptoclinides rufus* (Sluiter); *Polysyncrator aspiculatum* Tokioka; *Didemnum candidum* Savigny; *Didemnum moseleyi* (Herdman); *Amphicarpa diptycha* (Hartmeyer); *Polycarpa pedunculata* (Heller); *Cnemidocarpa etheridgii* (Herdman) (absent only from tropical Australia); *Herdmania momus* (Savigny).
4. *Southern and eastern Australian species.*
Ascidia aelara Kott; *Styela pedata* (Herdman); *Pyura pachydermatina* (Herdman) *gibbosa* (Heller); *Pyura spinifera* (Quoy and Gaimard); *Microcosmus nichollsi* Kott (absent only from tropical Australia).

The apparently endemic species comprise a considerable component (31%) of the fauna in the northern part of the Great Australian Bight. The circum-Australian forms comprise almost 50% of the species, while species with a range to Port Jackson (*Pyura p. gibbosa*, *P. spinifera*) or Moreton Bay (*Ascidia aelara*, *Styela pedata*, *Microcosmus nichollsi*) also occur. The three latter records extend the known range to the west, although the first two species are already known to occur in southwestern Australia. The data that are

recorded here do not therefore disagree with previous information (Kott 1972b) that supports the existence of a marine faunal Province extending from Cockburn Sound (or further to the north) on the western Australian coast to the vicinity of the eastern coast of South Australia.

There is no evidence that would suggest that the sample that is available is not typical of the fauna of the Great Australian Bight. This fauna, however, does not, on the basis of available data, appear to be typical of the Flindersian marine faunal Province. Apart from the large endemic component, the species occurring there have a wide distribution around the Australian coast, especially along the eastern seaboard. The species that terminate their range at the eastern end of the Flindersian Province have not been taken in these collections from the northern part of the Great Australian Bight (Kott 1972b), although they have been recorded at more easterly locations off South Australia.

Other species in this collection taken from other locations off the South Australian coast may be grouped according to the South Australian limits of their range in the following way:

1. *Species that do not extend eastwards into the Maugeat marine Province.*
Podoclavella cylindrica (Quoy & Gaimard); *Pycnoclavella diminuta* (Kott); *Alapozoa marshii* Brewin; *Diplosoma transluceidum* Hartmeyer; *Polyclinum neptunium* (Hartmeyer); *Stolonica carnosus* Millar; *Molgula sabulosa* Kott.
2. *Species that do not extend westwards into the Flindersian marine Province.*
Distaplia australiensis Brewin; *Eubherdmania australis* Kott; *Aplidium confertum* Kott; *Aplidium amorphatum* Kott; *Ascidia thompsoni* Kott; *Polyandrocarpa lapidosa* (Herdman); *Pyura irregularis* (Herdman); *Polycarpa tinctor* (Quoy & Gaimard); *Polycarpa papillata* (Sluiter).
3. *Species for which the Flindersian/Maugeat boundary does not comprise a barrier.*
Sycosia cerebriiformis (Quoy & Gaimard); *Sycosia pedunculata* (Quoy & Gaimard); *Ritterella herdmaniae* Kott; *Trididemnum savignii* (Herdman); *Trididemnum cerebriiforme* (Hartmeyer); *Symplegma viride* Herdman; *Pyura australis* (Quoy & Gaimard); *Microcosmus stolonifera* Kott.
4. *Gulf fauna.*
Pyura scoresbiensis Kott.

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Appendix—Station List

- NORTHERN GREAT AUSTRALIAN BIGHT** (32°24'S, 133°30'E). May 1973, Experimental Prawn Trawl, Explorer (Coll. P. Symond).
- 42 m: *Polycitor giganteum*
Patridium pulvinatum n. gen. n. sp.
Aplidium coeloides
Aplidium foliorum n. sp.
Leptoclinides volvus n. sp.
Herdmania momus
- 49 m: *Aplidium coeloides*
Aplidium flavolineatum
Aplidium digitatum n. sp.
Leptoclinides reticulatus
Polysyncrator aspiciulatum
Didemnum candidum
Didemnum moseleyi
Amphicarpa diptycha
Polycarpa pedunculata
Styela pedata
Cnemidocarpa etheridgii
Pyura pachydermatina gibbosa
Pyura spinifera
Herdmania momus
Microcosmus ticholli
- GOAT ISLAND**, off Ceduna, Great Australian Bight (Coll. P. Howlett).
- 32 m: *Ascidia aclara*
Pyura tendata
Microcosmus planus n. sp.
- ELLISTON BAY**, Feb. 1971 (Coll. S. A. Shepherd).
- Outside bar:
Euherdmania australis
Ritterella herdmania
Aplidium amorphatum
Leptoclinides rufus
Oculinaria australis
- Reef: *Symplegma viride*
Aplidium coniferium
- Vertical faces (25 m): *Pyura pachydermatina*
Molgula sabulosa
- WEST ISLAND**: Amphitheatre Rock
- 7 m deep, 13.vii.1972:
Polycitor giganteum
- 17 m deep, 12.vii.1972:
Sycosoa cerebriiformis
- CAPE JAFFA**: Margaret Brock Reef (3-4 m deep and in caves), 28.xi.1972.
Pseudodistoma cereum
- INVESTIGATOR STRAIT**, January, 1971 (Coll. J. E. Watson).
- Station XI (depth 19 m):
Aplidium prorum n. sp.
Diplosoma translucidum
Pyura australis
- Station X3:
Pyura australis
- Station X7:
Herdmania momus
- Stations X8, X9, X10:
Pyura scoresbiensis
- Station Y1:
?Polyclinum neptunium
Stolonica carnosa
Polyandrocampa lapidosa
Molgula mollis
- Station Y5:
Atapozoa marshi
Euherdmania australis
?Polysyncrator aspiciulatum
Pyura australis
- Station Z6:
Atapozoa marshi
- UPPER SPENCER GULF**, September, 1973. Transects and stations of S. A. Shepherd, Department of Fisheries, S. Aust.
- Transects A-D:
Polycarpa pedunculata (arenaceous and naked specimens, sometimes growing side by side, attached to the same shell or stone, stalked or sessile).
- Station A1 on Pinna, depth 0-1 m:
Pyura irregularis
Pyura vittata
- Station A5, depth 17 m:
Ascidia thompsoni
Polycarpa pedunculata
- Station A7, depth 10 m:
Polycarpa pedunculata (2 spec.)
- Station B4, depth 17 m:
Sycosoa pedunculata
- Station B7, depth 5 m:
Polycarpa pedunculata (some naked, black; a few leathery)
Polycarpa papillata (single specimen)
Pyura irregularis (one small aggregate)

- Station B10, depth 10 m, channel:
Polycarpa tinctor
Molgula mollis
- Station C4, depth 12 m:
Polycarpa pedunculata (naked and arena-
 ceous)
- Station D3, depth 18 m:
Ascidia thompsoni
- Station D5, depth 15 m:
Distaplia australiensis
- Station D9, depth 10 m:
Pyura scoresbiensis
- Station E1, depth 7 m:
Polycarpa pedunculata
Microcosmus nicholli
Microcosmus stolonifera
- Station F3, depth 9 m:
Ascidia thompsoni
- Station E4, depth 5m:
Pyura irregularis
- Station F1, depth 19m:
Polycarpa pedunculata (small stalked,
 arenaceous)
- Station F3, depth 19 m:
Pyura scoresbiensis (without stalk)
- Station F4, depth 16 m:
Ascidia thompsoni (with barnacles)
- Station G, depth 9 m:
Ascidia thompsoni
- Parabotryllus nemorus* n. gen., n. sp.
Polycarpa pedunculata
Pyura scoresbiensis
Halocynthia hispidula
Microcosmus squamiger
Herdmania momus
- Reef, 4 km NNW Douglas Bank:
Podoclavella cylindrica
Pyura australis
- SPENCER GULF.
- Tipara Reef, depth 11 m, 24.ix.1971:
Pycnoclavella diminuta
Pyura irregularis
- Under stones:
Herdmania momus
- Depth 5 m, 2.v.1972:
Podoclavella cylindrica
- ST VINCENT GULF.
- Port River (near Electricity Trust), depth 3 m,
 muddy bottom, 9.vi.1972:
Styela plicata
- Outer Harbour:
Pyura stolonifera
Microcosmus squamiger
- Sellick Beach (S of Adelaide), Feb. 1972 (Coll.
 R. Hammond):
Trididemnum savignii
Trididemnum cerebriforme

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NOTES ON THE GENUS *PSEUDOMALAXIS* FISCHER (MOLLUSCA: GASTROPODA) AND ITS FOSSIL SPECIES IN AUSTRALIA

BY M. F. BUONAIUTO*

Summary

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The possible synonymous or subgeneric relationship of *Mangonuia* Mestayer to *Pseudomalaxis* Fischer, of *Calodisculus* Rehder to *Awarua* Mestayer, and of *Claraxis* Iredale to *Torinista* Iredale, are considered.

Introduction

The genus *Pseudomalaxis* Fischer is represented in Australia only by three known species, two fossil and one living; the Late Eocene *P. asculpturatus* Maxwell, 1966; the Miocene *P. praemeridionalis* (Chapman, 1912); and the living *P. meridionalis* (Hedley, 1903). Only the two fossil species will be discussed and described here. However, it is necessary to discuss (a) the taxonomy of the genus *Pseudomalaxis* and the related genera *Mangonuia* and *Awarua* Mestayer; (b) in which family the genus should be placed.

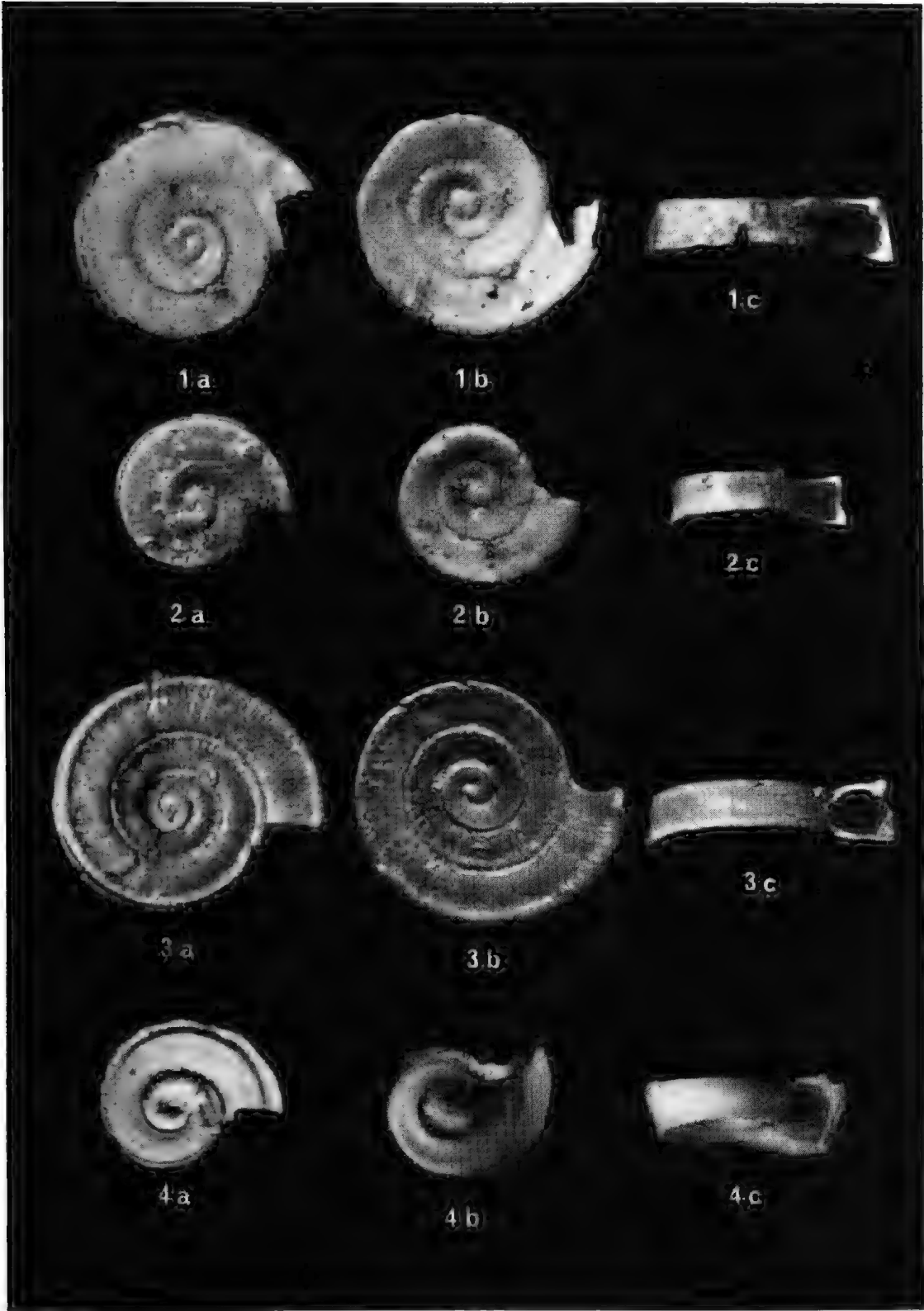
(a) Fischer (1885, p. 714) found in a living form, then referred to the Neogene *Bifrontia zancalea* (Philippi), a torinioid operculum and therefore instituted for it *Pseudomalaxis* as a new subgenus of *Torinia* Gray. Sacco (1892, p. 75) considered *Pseudomalaxis* Fischer a subgenus of *Discohelix* Dunker. Dall (1892, p. 331) recognized the intrageneric relationships between the Recent American *Omalaxis nobilis* Verrill and *P. zancalea* (Philippi), but instituted *Discosolis* for *O. nobilis* as a section or possible subgenus of *Discohelix*, because of Verrill's description of the operculum of *O. nobilis* as trochoid. Iredale (1911, pp. 253-7) tidied up the confusion existing in the use of the names *Discohelix* Dunker, *Omalaxis* Deshayes, *Bifrontia* Deshayes, and *Pseudomalaxis* Fischer; he placed *Bifrontia* in syno-

nymy with *Omalaxis*, and separated the three remaining genera as distinct taxa. Also, he distinguished one of the two living forms previously referred to *P. zancalea* (Philippi) as a different species, *P. macandrewi* Iredale, because of the latter's more evolute coiling, and restricted *Pseudomalaxis* to this new living form.

Later, Monterosato (1913, pp. 362-3), from a different viewpoint, restored *P. zancalea* as type-species of *Pseudomalaxis* and described the other living Mediterranean form, *P. actoni* Monterosato, previously mistaken by authors for *P. zancalea*. Monterosato also instituted for the above evolute form the subgenus *Spirolaxis* with *P. (Spirolaxis) centrifuga* Monterosato, 1890 (syn *P. macandrewi* Iredale, 1911) as type-species (Monterosato 1913, fig. 2). Cossmann (1915, pp. 122, 141) restricted *Discohelix* Dunker to the Mesozoic forms and *Pseudomalaxis* to the Cretaceous-Recent, referred both to Euomphalinae, and separated *Omalaxis* Deshayes in the Omalaxinae, a new subfamily.

Rehder (1935, p. 129) recognized a very close affinity between *Discosolis nobilis* (Verrill) and *Pseudomalaxis actoni* Monterosato and therefore placed *Discosolis* Dall in synonymy with *Pseudomalaxis* s. str. Rehder (1973, pers. comm.) remarks: "*Mangonuia* Mestayer, 1930, is probably a junior synonym

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or at least a subgenus of *Pseudomalaxis* Fischer, 1885". Mestayer (1930, pp. 144-5) refers *P. meridionalis* (Hedley) to *Mangonula*. In fact, the recent *Mangonula hollansi* Mestayer, the type of this genus, displays the general pattern of spiral ornaments, the quadrangular outer and the subcircular inner shape of body whorl characteristic of the Neogene-Recent *Pseudomalaxis* s. str., described below, and the same type of pseudoplanispiral coiling of this group.

Rehder, further comments, "*Calodisculus* Rehder, 1935, is very close to *Awarua* Mestayer, 1930, and is probably its synonym". Wenz (1939, p. 667) considers *Awarua* a subgenus of *Mangonula*. However, *Calodisculus* and *Awarua* display the same kind of specialization in spiral ornaments, in particular a marked development of heavily beaded circum-umbilical cords. *Awarua amoena* (Murdoch & Suter) (Suter 1913, p. 318; 1915, pl. 15, fig. 21 a-b) displays also a torinoid operculum (Mestayer 1930, p. 146).

"*Claraxis* and *Torinista* Iredale are very similar, possibly synonymous, and might be separated as a distinct genus which may be closer to *Heliculus* d'Orbigny". Wenz (1939, pp. 666, 668) considers the former two as subgenera of *Mangonula* and the latter as a synonym of *Torinista* Gray. In this case, *Claraxis* should fall into synonymy with *Torinista* because although Iredale (1936, p. 327) published their initial diagnoses on the same page, the former is described after the latter. From the original description and drawings of the type species, it is impossible to find substantial generic differences and Iredale did not specify any.

(b) The genus *Pseudomalaxis* Fischer is often placed in different families but generally is referred to the Architectonicidae. In introducing the genus, Fischer referred it to the Solariidae (= Architectonicidae) on the basis of the conical torinoid operculum (Fischer 1885, p. 714; see also Earnes 1952, p. 37), observed in the Recent form *P. (Spirolaxis) centrifuga* Monterosato (Monterosato 1890) and in *P.*

nobilis (Verrill) (Verrill 1885, p. 423, pl. 44, fig. 12).

Iredale (1936, p. 326) instituted a new family Mangonulidae for the Australasian genera *Mangonula*, *Awarua*, *Torinista* and *Claraxis*. Apparently, Wenz (1939) considered Mangonulidae synonymous with the Architectonicidae. Because of a certain affinity between the opercula of *P. balesi* Pilsbry & McGinty and *Parviturbo zacalles* (Mazyck), Pilsbry & McGinty (1945, pp. 9, 57, pl. 6, figs 2-2a, 5) placed *Pseudomalaxis* in the Cyclostrematidae. Later, Abbott (1954, p. 138) included *Pseudomalaxis* in Vitrinellidae on the basis of a vague and incorrect reference to a revision of the family by Pilsbry. Maxwell (1966, p. 444) followed Abbott.

Rehder (1974, pers. comm.) gave the opinion: "I have examined young specimens of both *Pseudomalaxis* and *Architectonica* (*Pslaxis*), and I can find no essential difference in their protoconchs; both show a heterostrophic-anastrophic protoconch. I feel, therefore, that *Pseudomalaxis* should remain in the Architectonicidae". There is support for this statement both on the basis of the torinoid conical operculum and the protoconch coiling of *Pseudomalaxis*. Therefore the author, in agreement with Rehder, regards the restoration of *Pseudomalaxis* Fischer to the Architectonicidae to be justified.

Collections

The specimens of *P. asculpturatus* Maxwell here studied are kept in the Palaeontological Section of the New Zealand Geological Survey (NZGS), and in the Department of Mines of South Australia (GSSA). The figured specimen of *P. praemeridionalis* (Chapman) is kept in the Palaeontological collection of the South Australian Museum of Natural History (SAM).

Specimens M3298 and M3299 were found by the author and specimens M3300-M3303 were found subsequently by J. M. Lindsay.

Fig. 1. *Pseudomalaxis (Pseudomalaxis) asculpturatus* Maxwell. McCullough's Bridge, New Zealand. NZGS, 9508-2; a, adapical; b, abapical; c, axial views (all X 17.50).

Fig. 2. *P. (Pseudomalaxis) asculpturatus* Maxwell. McCullough's Bridge, New Zealand, NZGS, 9508-1; a, adapical; b, abapical; c, axial views (all X 17.3).

Fig. 3. *P. (Pseudomalaxis) asculpturatus* Maxwell. Adelaide Plains Sub-Basin, Adelaide Children's Hospital Bore No. 5; GSSA, M3299; a, adapical (X 16); b, abapical (X 16); c, axial views (X 15).

Fig. 4. *P. (Pseudomalaxis) praemeridionalis* Chapman. Clifton Bank, Muddy Creek; SAM, P18342; a, adapical (X 10.6); b, abapical (X 10.6); c, axial views (X 12.3).

Synopsis of the history of the genus Pseudomalaxis Fischer on the basis of the major authors.

| Author | Family | Subfamily | Genus | Subgenus |
|--|--|--------------|--|--|
| Fischer (1885, p. 714) | Solariidae | — | <i>Torinia</i> Gray | <i>Pseudomalaxis</i> Fischer |
| Sacco (1892, p. 75) | Solariidae | — | <i>Discohelix</i> Dunker | <i>Pseudomalaxis</i> |
| Dall (1892, p. 331) | Solariidae | — | <i>Discohelix</i> | <i>Pseudomalaxis</i> <i>Discosolis</i> Dall |
| Iredale (1911, pp. 253-7) | Solariidae (?) | — | <i>Pseudomalaxis</i> <i>Discohelix</i> | <i>Pseudomalaxis</i> <i>Discohelix</i> <i>Discosolis</i> |
| Monterosato (1913, pp. 362-3) | Solariidae | — | <i>Pseudomalaxis</i> | <i>Pseudomalaxis</i> <i>Spirolaxis</i> Monterosato |
| Cossmann (1915, pp. 122, 141) | Euomphalidae | Euomphalinae | <i>Pseudomalaxis</i> | <i>Pseudomalaxis</i> |
| Mestayer (1930, p. 144) | Architectonicidae (syn. Solariidae) | — | <i>Mangonulia</i> Mestayer <i>Awarua</i> Mestayer | — — |
| Rehder (1935, p. 128) | Architectonicidae (?) | — | <i>Pseudomalaxis</i> | <i>Pseudomalaxis</i> (syn. <i>Discosolis</i> Dall) <i>Paurodiscus</i> Rehder <i>Calodisculus</i> Rehder |
| Iredale (1936, p. 326) | Mangonuliidae | — | <i>Mangonulia</i> <i>Awarua</i> | — |
| Wenz (1939, p. 668) | Architectonicidae (syns Solariidae, Mangonuliidae) | — | <i>Mangonulia</i> <i>Pseudomalaxis</i> | <i>Mangonulia</i> <i>Awarua</i> <i>Pseudomalaxis</i> <i>Spirolaxis</i> <i>Paurodiscus</i> <i>Calodisculus</i> |
| Pilsbry & McGinty (1945, p. 9) | Cyclostrematidae | — | <i>Pseudomalaxis</i> | <i>Pseudomalaxis</i> |
| Flamés (1952, p. 37) | Architectonicidae | — | <i>Pseudomalaxis</i> | <i>Pseudomalaxis</i> |
| Abbott (1954, pp. 138-9) | Vitrinellidae | — | <i>Pseudomalaxis</i> | <i>Pseudomalaxis</i> |
| Pchelintsev & Korobkov (1960, pp. 137-8) | Solariidae | — | <i>Pseudomalaxis</i> | <i>Pseudomalaxis</i> |
| Maxwell (1966, p. 444) | Vitrinellidae | — | <i>Pseudomalaxis</i> | <i>Pseudomalaxis</i> |
| Glibert (1973, p. 30) | Architectonicidae | — | <i>Pseudomalaxis</i> | <i>Pseudomalaxis</i> |
| This paper | Architectonicidae | — | <i>Pseudomalaxis</i> | <i>Pseudomalaxis</i> (syn. <i>Mangonulia</i>) ? <i>Mangonulia</i> <i>Spirolaxis</i> <i>Paurodiscus</i> <i>Awarua</i> (syn. <i>Calodisculus</i>) ? <i>Calodisculus</i> |

Systematic Descriptions

Phylum MOLLUSCA

Class GASTROPODA

Order MESOGASTROPODA

Superfamily CERITHACEA

Family ARCHITECTONICIDAE

Genus PSEUDOMALAXIS Fischer, 1885

Diagnosis: Shell discoidal, pseudoplanispiral; abapical side concave to subconcave, adapical

flattened to subconcave; outer shape of the body-whorl rectangular to quadrangular, inner shape subcircular to similar to the outer; thin margins, two carinae at abaxial-adapical and abaxial-abapical ends. Straight growth lines between the abaxial keels. Aperture rectangular to quadrangular; protoconch heterostrophic-anastrophic; operculum torinioid, thin, multi-spiral, outside flat or conical (after Wenz 1939, p. 668).

Subgenus *Pseudomalaxis* s. str.

Diagnosis: Shell medium-large to very small; margins thin; pseudoplanispiral with tangent whorls; suture flush to subimbricated; two adapical and two abapical keels; the four keels can be smooth or crenulated; growth lines a little irregularly packed; operculum flat (after Wenz 1939).

Observations: *Pseudomalaxis* s. str. appears to be represented in the Tertiary by two main forms. The first, predominant in the Eocene-Oligocene, is commonly characterized by growth lines and the four carinae as the only ornaments; a few species bear also spiral ornaments of fine riblets as in the Eocene *P. dixonii* (Vasseur) and the Oligocene *P. italica* (Sacco), or of beaded cords and keels as in *P. texana* (Aldrich); the outer shape of the body whorl is rectangular to quadrangular, the inner is subcircular to subquadrangular, the inner is subcircular to subquadrangular or subrectangular, depending on the thickness of the margins (the latter characteristic could be ontogenetic and related to age).

The second form, predominant in the Neogene-Recent, is characterized by the development of a main spiral rib or cord on the abaxial region of the adapical margin, and often of spiral costellae on the abaxial margin. The four carinae and the adapical rib usually bear heads or short spines. The outer shape of the body

whorl is commonly quadrangular to subquadrangular, the inner shape is subcircular.

***Pseudomalaxis* (*Pseudomalaxis*) *asculpturatus* Maxwell, 1966**

FIGS 1-3

1966 *Pseudomalaxis asculpturatus* Maxwell, p. 444, figs 11-13.

Material: 4 specimens very well preserved with the peristome slightly damaged (GSSA, M3298-9; NZGS, 9508-1, 9508-2) and another 4 juvenile or damaged (GSSA, M3300-3).

Description: Shell very small and thin, biconcave, nearly planispiral; protoconch heterostrophic-anastrophic; whorls increasing far more in diameter than in height and overlapping entirely in relation to the coiling axis and very scarcely in relation to the normal to it. Suture flush to subimbricated. Body-whorl shape: outer subquadrate-subtrapezoidal; inner subcircular-ovoidal, wider than high. Whorl regions: adapical and abapical subconvex; abaxial flattened or subconcave, nearly vertical. Body-whorl regions connected by prominent smooth abaxial carinae. Abapical side more concave than the adapical one.

Ornaments: Growth lines and rugae, prosocline in the adapical and abaxial regions, opisthocyt in the abapical. Four carinae: at abaxial-adapical, abaxial-abapical, adaxial-adapical, and adaxial-abapical ends.

DIMENSIONS (in mm): (see Fig. 5)

| Specimen | No. whorls | Dw | N | Nis | Hw | Lis | Hgc | Dgc |
|-------------|------------|------|------|------|------|-------|------|------|
| M3298 | 4 | 2.55 | 0.95 | 0.40 | 0.50 | -0.10 | 0.60 | 0.65 |
| M3299 | 4 | 2.50 | 0.92 | 0.39 | 0.55 | -0.10 | 0.65 | 0.60 |
| NZGS 9508-1 | 3 | 1.55 | 0.70 | 0.30 | 0.40 | -0.05 | 0.45 | 0.50 |
| NZGS 9508-2 | 3 | 2.15 | 0.90 | 0.35 | 0.58 | 0.00 | 0.58 | 0.50 |

RATIOS: (see Fig. 5)

| Specimen | Hw/Dw | K = Lis/Hw | v = Nis/N | Hgc/Dgc |
|-------------|--------|------------|-----------|---------|
| M3298 | 0.1961 | -0.2000 | 0.4211 | 0.9231 |
| M3299 | 0.2200 | -0.1818 | 0.4239 | 1.0833 |
| NZGS 9508-1 | 0.2581 | -0.1250 | 0.4286 | 0.9000 |
| NZGS 9508-2 | 0.2698 | 0.0000 | 0.3889 | 1.1600 |

Localities: Adelaide Plains Sub-Basin (St Vincent Basin, S. Aust.); Adelaide Children's Hospital, North Adelaide, hundred of Yatala, Town Acre 717, Bore 5, at 20.42-20.75 m (M3298) and 21.64-21.95 m (M3299); Bore 2, at 22.25-22.56 m (M3302, M3303); Adelaide Metropolitan Subway, Bore 3, north bank

of Torrens Lake, opposite Kintore Avenue, at 20.10 m (M3300) and 24.50 m (M3301) New Zealand; McCullough's Bridge.

Stratigraphic Distribution: Adelaide Plains Sub-Basin: Lindsay (1966) gave a brief stratigraphic summary of Adelaide Children's Hospital Bores 2 and 5. "The interval 20.42-21.95

m in Bore 5 is low in Blanche Point Marls (Aldingan, Late Eocene). The *Hantkenina primitiva* zone occurs in this bore at 19.20–19.51 m, i.e. slightly above *P. asculpturatus*. In the type section at Maslin Bay, *Hantkenina primitiva* is present only in a restricted band 0.80–1.15 m above the base of Blanche Point Transitional Marls.

Other specimens from Adelaide Children's Hospital, Bore 2, are within the *Hantkenina primitiva* zone. Although *H. primitiva* has not yet been found in Adelaide Metropolitan Subway Bore 3, the specimens of *P. asculpturatus*

are certainly from near, and probably from slightly above, the *H. primitiva* zone.

Thus the vertical distribution of all the specimens of *P. asculpturatus* found in the Adelaide area spans a narrow interval from slightly below to probably slightly above the *H. primitiva* zone, in Blanche Point Transitional Marls, Late Eocene." (J. M. Lindsay, Dept of Mines, pers. comm., 1974.)

New Zealand: Upper Waihao Greensand, Kaiatan, Late Eocene.

Observations: The two Australian specimens show an inversion in the coiling, variable in

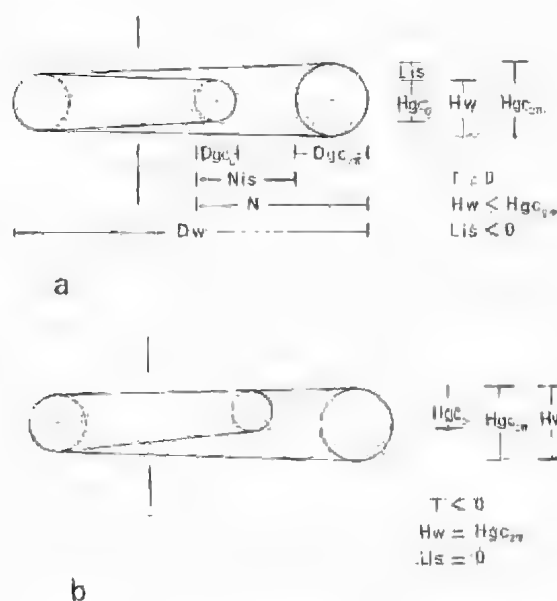


Fig. 5. The parameters measured in planispiral (a) and in pseudoplanispiral (b) gastropod shell are here defined as follows:

N or w : the total number of the whorls, as the total number of revolutions of the generating curve around the coiling axis.

Hw : height of any whorl (in this case the last one) as the projection of the coiling axis of the distance between the adapical point of the generating curve at the initial position and its abapical point at the final position after a 2π revolution in the given interval $2n\pi - 2(n+1)\pi$.

Lis : intersutural height of any whorl as the projection on the coiling axis of the distance between the initial and final position of a given point placed on the adapical line of the body whorl after a 2π revolution, where the adapical line is the geometrical locus of any point placed at the adapical end of the generating curve.

Hgc : the height of the generating curve as projection on the coiling axis of the distance between its adapical and its abapical points.

Dw : the maximum diameter of any whorl as the projection on the normal to the coiling axis of the part of the planispiral or helicoid cone produced by the generating curve after a π revolution and included in the given interval $(2n+1)\pi - 2(n+1)\pi$.

N : as the projection on the normal to the coiling axis of the distance between the adaxial point of the generating curve at $2n\pi$ and its abaxial point at $2(n+1)\pi$ position.

Nis : intersutural distance as the projection on the normal to the coiling axis of the distance between the initial and the final position of a point placed on the adaxial line after a 2π revolution, where the adaxial line is the geometrical locus of any point placed at the adaxial end of the generating curve.

Dgc : diameter of the generating curve as the projection on the normal to the c. axis of the distance between its adaxial and its abaxial point.

The generating curve is here considered the projection on a plane, containing entirely the coiling axis, of the outline of the growing edge of a gastropod shell. The body whorl here represents the part of shell cone generated by the growing edge in a given interval $2n\pi - 2(n+1)\pi$. T is the translation of the generating curve along the coiling axis per revolution. K and v are respectively the indexes of overlapping of any whorl; K , parallel to the coiling axis; v , normal to the coiling axis, and are defined by the ratios $K = Lis/Hw$ and $v = Nis/N$. (After Raup 1966. Observations consistent with this theory will be presented in a subsequent publication.)

amount, from a more helicoidal protoconch to a more planispiral teleoconch. Undescribed in Australia, this form was directly compared with two topotypes of the only coeval species of *Pseudomalaxis* known in Australasia, *P. asculpturatus* Maxwell. These two topotypes, more juvenile than the Australian ones, display a somewhat higher spire, producing a decreasing concavity and consequent flattening of the adapical side, as a result of the same inversion of the coiling; fainter carinae, but the younger of the two has them more marked. Protoconch, growth lines, outer and inner shape of the body whorl are the same. Because the amount of inversion in the coiling of the New Zealand forms appears to differ only slightly from that of the Australian forms, and is also variable in the Australian and New Zealand specimens, it is very difficult to distinguish at the specific level between these two forms. Hence, they are here considered conspecific and representing probably different geographical morphs.

From *P. asculpturatus* Maxwell, the Anglo-Parisian Eocene *P. dixonii* (Vasseur) (Cossmann 1915, pp. 142-3), differs by its higher spire and presence of spiral riblets; the Proto-Adriatic Priabonian *P. heyrichi* (Oppenheim, 1896) by its much higher spire and an abaxial margin abapically more convergent to the axis; the Liguria-Piemonte Middle Oligocene *P. italicus* Sacco, 1892, by its lower spire and by the presence of spiral riblets. The Indian Eocene *P. punjabensis* Eames, 1952, seems on the contrary very close, but the holotype being very juvenile and the original illustration very poor, it is impossible to determine the actual differences and affinities between them.

The American Claiborne Eocene *P. rotella* (Lea) (Palmer 1937, p. 176) differs by its rectangular aperture, higher spire, and lesser number of whorls; *P. texana* (Aldrich) (Palmer 1937, p. 178) by crenulated abaxial keels and spiral cords on the adapical margin; and *P. plummerae* Palmer (Palmer 1937, p. 178, by subelliptical margins, more imbricated sutures, and the adoral part of the last whorl twisted to the adapical.

Other Eocene species (Cossmann 1915) are the Anglo-Parisian *P. patellatus* (Sowerby), and the Egyptian *P. lybicus* (Oppenheim).

Maxwell (Nov. 1974, pers. comm.) states: "Two specimens of a *Pseudomalaxis* have recently been obtained from a Mangarapan

(Lower Eocene) sample from North Canterbury. The material is not well preserved but the shells closely resemble *P. asculpturatus* except for their much smaller size (the larger specimen is only 1 mm in diameter). I don't think that the Lower Eocene shells are juveniles of *P. asculpturatus*, however, as they also have much smaller protoconchs".

He quotes also the occurrence of *P. cf. asculpturatus* Maxwell from Wharekuri, South Canterbury (Dunroonian, Oligocene) (Maxwell 1969, p. 161) but "The sole specimen is broken", however it "is certainly close to the Eocene species".

Pseudomalaxis (*Pseudomalaxis*) *praemeridionalis* (Chapman, 1912)

FIG. 4

1912 *Homalaxis praemeridionalis* Chapman, p. 186, pl. 12, figs 4-6.

Material: 1 specimen very well preserved (SAM, P18342).

Description: Shell small, thin, planoconcave, pseudoplanispiral, with the adapical side flattened and the abapical concave; whorls increasing far more in diameter than in height and overlapping entirely in relation to the coiling axis and very scarcely to the normal to it. Heterostrophic-anastrophic protoconch with three smooth whorls; the inversion of the coiling already displayed in the third whorl. Suture grooved. Body-whorl shape: outer subquadrate-trapezoidal; inner subcircular-ovoidal; slightly wider than high. Body whorl regions: adapical convex in the adaxial part, concave in the abaxial; abaxial flattened; abapical convex; aperture with subquadrate peristome. Lips: adapical elliptical with a gutter-shaped reflection in the middle; parietal and abaxial straight; abapical elliptical. Lip and region connections angular, marked by carinae.

Ornaments: Four spiral beaded carinae, the abaxial ones with very short axially elongated spines: adaxial-adapical, adaxial-abapical, abaxial-adapical, abaxial-abapical; a spiral crenulated cord on the abaxial part of the adapical region and a smooth costella on the adapical part of the abaxial region. Growth lines: prosocline in the adapical region; prosocline in the abaxial; orthocyr in the abapical.

DIMENSIONS (in mm): (see Fig. 5)

| No. whorls | Dw | N | Nis | Hw | Ls | Hgc | Dgc |
|------------|-----|-----|------|------|-------|------|------|
| 4 | 2.6 | 1.3 | 0.45 | 0.88 | -0.02 | 0.90 | 0.98 |

RATIOS:

| Hw/Dw | K | Lis/HW | v = Nis/N | Hgc/Dgc |
|--------|---------|--------|-----------|---------|
| 0.3384 | —0.0227 | | 0.3461 | 0.9184 |

Localities and Stratigraphic Distribution: Muddy Creek Marls, Clifton Bank, Muddy Creek, 6.4 km west of Hamilton; "blue clays", Newport Formation, Altona Bay Coal Shalt. Vic.

Stratigraphic Range: Balcombian, Early Middle Miocene (Ludbrook 1973).

Observations: *P. praemeridionalis* (Chapman) was referred to Darragh (1970, p. 188) to *Mangonia* Mestayer. The specimen here described represents the second discovery of this species. From *P. praemeridionalis*, the Paleo-Mediterranean Neogene *P. zancaea* (Philippi) (Wenz 1939, p. 668, fig. 1906) differs by a slimmer body-whorl, higher spire, adapical spiral costa closer to the adapical-abaxial carina, absence of spiral riblets on the abaxial margin; from the Paleo-Mediterranean Pliocene *P. uldravandi* (Foresti) (Sacco 1892, p. 75, pl. 2, fig. 65 a-d, 65 bis a-d) by smooth adapical-abaxial carina, absence of spiral abaxial riblets, higher spire, and adapical costa closer to the adapical-abaxial carina; from the Parathetys Miocene *P. boettgeri* Cossmann (Cossmann 1915, p. 143) by a larger body-whorl, lower spire, lesser number of whorls, lack of spiral ornaments except rarely, beaded abaxial carinae, a semi-circular inner shape of the body whorl; from the Mediterranean Recent *P. actoni* Monterosato (1913, p. 362) by a greater number of whorls, slimmer body-whorl, lower spire, more marked growth lines, more abaxial riblets, and an abaxial margin more parallel to the coiling axis. The Australian Recent *P. meri-*

dionalis (Hedley) (Hedley 1903, p. 351) displays, on the other hand, a very close affinity to *P. praemeridionalis* (Chapman), differing from it only by two more abaxial riblets and the abapical-adaxial carina with heavier beads.

The New Zealand Recent ?*P. bollonsi* (Mestayer, 1930, p. 144) differs by more whorls, two beaded abaxial cords, broader abapical-abaxial carina and slightly opisthocline growth lines on the adapical region.

The American Recent *P. nobilis* (Verrill) (Verrill 1885, p. 423, pl. 44, fig. 12) differs by its shorter spire, a greater number of whorls, slimmer body-whorl, adapical cord closer to the abaxial-adapical carina, five spiral ribs on the abaxial margin, and fine spiral ribs on the abapical margin.

Acknowledgments

I am very grateful to Dr P. A. Maxwell of the Geological Survey of New Zealand for his assistance, particularly in lending topotypes of *Pseudomalaxis usculpturatus*; to the Director of Mines, South Australia, for the loan of material; to Dr H. A. Rehder, National Museum of Natural History, Smithsonian Institution, for the information on taxonomy; to Dr H. Silcock, Department of Pure Mathematics, University of Adelaide, for verifying the definitions of the paramenters; to Dr N. H. Ludbrook for encouragement and for reading the manuscript. The work was carried out in the Department of Geology and Mineralogy, University of Adelaide, during tenure of a University Research Grant.

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THE CLINGING MECHANISM OF *PSEUDOPHRYNE BIBRONI* (ANURA: LEPTODACTYLIDAE) TO AN ALGA ON GLASS

BY N. GRADWELL*

Summary

GRADWELL, N. (1975).-The clinging mechanism of *Pseudophryne bibroni* (Anura: Leptodactylidae) to an alga on glass. *Trans. R. Soc. S. Aust.* **99**(1), 31-34, 28 February, 1975.

Despite the absence of an oral sucker, tadpoles of all stages from 26 to 40 (of Gosner 1960) were found to be capable of clinging by their jaws to an alga on vertical glass. When the glass was wiped clean of the alga, *Phyllobium* sp., tadpoles were no longer able to attach themselves. Therefore substratum algae are necessary for the clinging of the tadpoles to glass.

As the nares appear to suffice as inhalent channels, the dental apparatus of tadpoles is adapted to maintain a firm grip on the alga. There is an absence of peripheral papillae adjacent to the most posterior of the tooth rows of the lower lip. Therefore this tooth row can bend farther forward and the security of its grip on the alga is probably increased.

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Introduction

It is well known that anuran tadpoles are adapted to occupy a wide variety of ecological niches (Noble 1931, Orton 1953). Of the morphological adaptations, an attachment mechanism for clinging to substrata is a predictable association with a lotic habitat. It is thus possible to avoid dislodgement by swift currents even in torrential streams. In contrast, the adhesive secretion produced by the ventral glands of most young embryos (at stages 18 to 24, of Gosner 1960) is too weak to withstand fast currents (Gradwell, unpublished). There is no published evidence that these glands can produce subambient hydrostatic pressures. They atrophy after stage 24, and in the tadpole which represents stages 25 to 40, either of two kinds of non-glandular sucker may develop.

An oral sucker is the most usual adaptation in lotic tadpoles and, accordingly, the degree of development of this sucker would seem to be influenced by the velocity of the ambient water. In most lotic species the periphery of the upper and lower lips is continuous and forms a suctional disc, and the number of tooth rows increases progressively with the velocity of the ambient water (Noble 1931; Gradwell, unpublished). The structure and function of a tadpole's oral sucker has been described in *Ascaphus truei* (Gradwell 1971, 1973) and it

has been compared with the suckers of five Australian species (Gradwell 1975). In addition, Tyler (1963) described the external appearance of the sucker of *Litoria arfakiana* (as *Hyla angularis*), which is much like that of *Ascaphus*.

Another type of tadpole sucker is that which lies posterior to the mouth. The anatomy of such a sucker has been described in *Staurois ricketti* by Noble (1931) and in *Staurois afghana* (Bhaduri 1935). No data are available on the magnitude of its suction, except that if a tadpole is manually lifted out of the water by its tail, its sucker can support a stone sixty times the weight of the tadpole (Hora 1922).

The present paper reports a mechanism employed by lentic tadpoles of the Australian leptodactylid frog *Pseudophryne bibroni* which enables them to cling to a vertical substratum, even though they lack a sucker. I have observed such ability in nature for many other suckerless tadpoles and have assumed that they use their teeth to secure a grip on rocks.

Results and Discussion

On 18 July 1974, 16 tadpoles of *Pseudophryne bibroni* (at stages 26 to 29) were collected in a flooded ditch (ca 30 m long by 5 m wide) with sides sloping to a depth of 2.5 m. This habitat is about a kilometre from Boyd

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Fig. 1. *A.* The tadpole of *Pseudophryne bibroni* (stage 36) clinging to algae on the vertical glass side of an aquarium. *B.* Oral apparatus of a clinging tadpole as seen through a thin transparent layer of the alga *Phyllobium* sp. growing on the aquarium glass. As the lower beak is enclosed within the upper beak, only the latter is visible. The lower labial teeth are inclined forward to grip the algae. Adduction is accomplished by a slight lateral compression of the lips and teeth. *C.* The oral apparatus dissected free from a tadpole to show the beaks in an open condition. Calibration bars = 1 mm.

River Crossing, near Jenolan Caves, N.S.W. The maximum depth of water was 0.5 m and the bottom consisted of mud and fallen *Eucalyptus* leaves and bark. At 3.00 p.m. the water temperature was 6 to 8°C. Five hours later, the tadpoles were placed in an aerated aquarium at approximately the same temperature.

For initial identification, the mouthparts of the tadpoles were examined and compared with the description of Martin (1965). Because the absence of a sucker was noted, it was surprising to observe that all of the tadpoles clung to the vertical glass sides of the aquarium (Fig. 1A). This attachment was insecure, for these tadpoles were sometimes displaced from their clinging sites when other tadpoles collided with them. Examination of the oral region of a clinging tadpole, by stereomicroscope through the glass, showed that the lower beak was kept closed within the edge of the upper beak (Fig. 1B) and that the upper and lower tooth rows were held adducted, though not touching one another. The nares were the only inhalant channels for gill irrigation.

During preparations for photography it was found that the inside of the glass aquarium was covered with a thin layer of algae which prevented sharp focussing on the mouth and teeth. Therefore, half of one side of the aquarium was cleaned of its algae, and a camera conveniently positioned to await the settling and clinging of a tadpole on the cleaned glass. Although tadpoles attempted to cling to the cleaned glass, they were unsuccessful. However, they cling readily to the uncleared glass, demonstrating the presence of algae on the glass to be necessary for the clinging of these tadpoles.

Apart from clinging to the glass, the tadpoles also showed frequent feeding movements over the glass during which their jaws opened and closed rhythmically in a scraping action. Figure 1C shows the jaws in an open condition and both the upper and lower beaks are visible. The predominant alga growing on the glass was *Phylloium* sp. (identified from Prescott 1970), which has a thallus of branched strands. At the ends of the strands are swellings called akinetes, which contain chloroplasts. It was of spe-

cial interest to find akinetes in the manicotho ("stomach") of tadpoles, which suggests that they had been grazed off the glass. It would also seem that the bulbous akinetes on their strand-like thallus could easily be gripped by the minute sharp teeth of tadpoles, thus providing anchorage. It is possible that other filamentous algae may also permit the clinging of these tadpoles to substrata.

There are no papillae behind the most posterior row of lower labial teeth. Therefore this row of teeth can bend farther forward than if papillae were present here and so the teeth can grip substratum plants more firmly. However, some other suckerless tadpoles (for example, *Lioria verreauxi*) can cling feebly to vertical substrata in similar fashion even though they lack a posterior gap in their peripheral papillae.

Four tadpoles were raised into juvenile frogs. Until stage 40, the tadpoles (entire length, 36.0 mm; snout-to-vent length, 17.4 mm) were able to cling by their teeth to the substratum. After this stage the beaks and teeth were shed prior to widening of the mouth.

It is proposed here that *Pseudophryne hibroni* tadpoles are able to cling to vertical substrata by biting their teeth into algae and perhaps other vegetation. As the narial inflows appear to be sufficient for respiration, the jaws need not open and close rhythmically to admit additional water, but can maintain their bite on plants. However, I have not had the opportunity to compare these findings with the ability of *P. hibroni* in their natural habitat to cling to substrata. The absence of an oral sucker in these tadpoles confers greater flexibility on the jaws and perhaps it broadens their food resources. On the other hand, an oral sucker in lotic tadpoles facilitates grazing on algae in swift currents (Gradwell 1971), where more tenacious gripping is needed.

Acknowledgements

I am grateful to Miss P. McDonnell and Mr B. Wilson for collecting the tadpoles, and to Miss M. Anstis for identifying them. Mr M. J. Tyler kindly read the manuscript and offered helpful suggestions.

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GENETIC EVIDENCE FOR THE EXISTENCE OF TWO SEPARATE POPULATIONS OF *RATTUS FUSCIPES GREYII* ON PEARSON ISLAND, SOUTH AUSTRALIA

BY L. H. SCHMITT*

Summary

SCHMITT, L. H. (1975).-Genetic evidence for the existence of two separate populations of *Rattus fuscipes greyii* on Pearson Island, South Australia. Trans. R. Soc. S. Aust. **99**(1), 35-38, 28 February 1975.

A study of genetic variation of the enzyme glutamate oxaloacetate transaminase (GOT) reveals the presence of two distinct populations of the southern bush-rat (*Rattus fuscipes greyii*) on Pearson Island. Two allelic genes, *Got-l^a* and *Got-l^b* are present in the animals collected from the middle and southern sections of the island, while *Got-l^a* is absent in animals taken on the northern section. This is discussed in relation to the Pearson Island wallaby which was, until recently, restricted to the northern section of the island.

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A study of genetic variation of the enzyme glutamate oxaloacetate transaminase (GOT) reveals the presence of two distinct populations of the southern bush-rat (*Rattus fuscipes greyii*) on Pearson Island. Two allelic genes, *Got-1^a* and *Got-1^b* are present in the animals collected from the middle and southern sections of the island, while *Got-1^a* is absent in animals taken on the northern section. This is discussed in relation to the Pearson Island wallaby, which was, until recently, restricted to the northern section of the island.

Introduction

Pearson Island, which lies 60 km off South Australia's west coast, is divided into three discrete sections (Fig. 1). The southern and middle sections are linked by a causeway, while the middle and northern sections are separated by a narrow sea channel. The total area of the island is approximately 325 hectares. The Pearson I. wallaby, *Petrogale* sp. (see Thomas & Delroy 1971, for a discussion on its taxonomic status) and the native rat, *Rattus fuscipes greyii*, are the only terrestrial mammals which are known to inhabit the island.

The native rat, which is found on all three sections of Pearson I., was first described by Thomas (1923) who named it *Rattus murrayi*. Iredale & Troughton (1934) reclassified it as *Rattus greyii murrayi* recognizing its close relationship to *Rattus greyii greyii*, the native bush-rat of mainland South Australia. It was later included in the species *Rattus fuscipes* by Ellerman (1949) as a distinct sub-species, *R. fuscipes murrayi*, along with the mainland form *R. f. greyii*. Recently, Taylor & Horner (1973a) have considered it to be subspecifically indistinguishable from *R. f. greyii*.

Until 1960, the Pearson I. wallaby was only found on the northern section of the island. No evidence could be found to suggest the species ever inhabited the other two sections, despite the suitable habitat available there. The channel appeared to act as a very effective barrier to

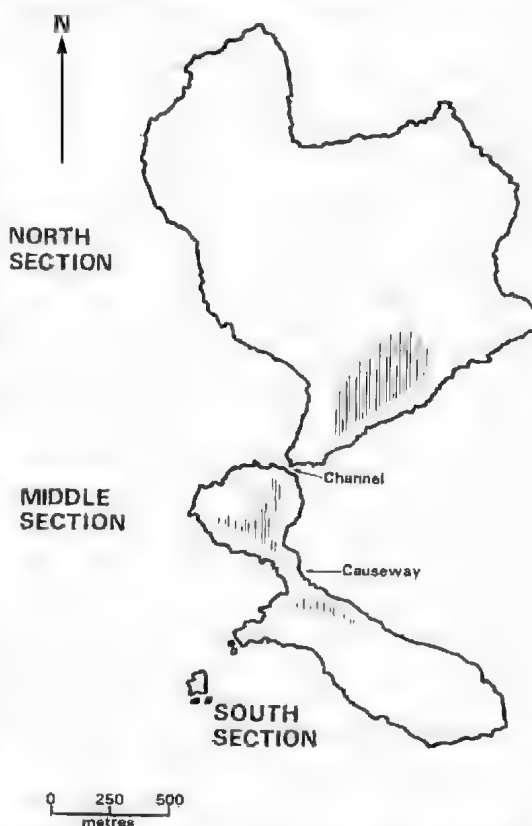


Fig. 1. Map of Pearson Island. Areas where animals were captured are indicated by shading.

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migration between the northern and middle sections. In 1960, six wallabies, including either four or five females, were accidentally released on the middle section and the species is now abundant on the middle and southern sections (Thomas & Delroy 1969).

This paper describes a genetic difference in the *R.f. greyii* population of Pearson I., apparently caused by a restriction in migration across the channel separating the northern and middle sections.

Methods

Specimens of *R.f. greyii* were caught in "Sherman" traps and transported alive to Adelaide. Tissue homogenates were prepared and subjected to starch gel electrophoresis. The electrophoretic buffers (pH 8.0) were essentially the same as those described by Selander *et al.* (1971). The methods used to detect glutamate oxaloacetate transaminase (GOT) activity and determine the subcellular locality of the isozymes were modified from those given by De Lorenzo & Ruddle (1970). Heart extracts were used predominantly, except in the latter procedure when liver extracts were used.

Results and Discussion

Animals were caught from the areas shown in Fig. 1. Seventy-five animals were caught in 218 trap nights, yielding a capture rate of 34%. This is considerably higher than the 2.8% return obtained by Taylor & Horner (1973b) for *R.f. greyii* on the mainland of Australia and Kangaroo I.

Two main regions of GOT activity were present in gels, one migrating cathodally, the other anodally. The cathodal area of activity consisted of a single invariant band. This isozyme predominated in mitochondrial extracts. The anodally migrating isozyme was found in the supernatant fraction and was variable. Three distinct phenotypes, GOT-1A, GOT-1B and GOT-1AB were observed. This variation is consistent with the active enzyme being a dimeric molecule and is similar to that found in man (Chen & Gihlett 1971) and the North American old-field mouse, *Peromyscus polionotus* (Selander *et al.* 1971). Genotypes can be assigned to each phenotype, presuming that the difference is under the control of an autosomal locus, with two co-dominant alleles. This locus has been designated *Got-1* and the alleles *Got-1^a* and *Got-1^b*.

Laboratory matings of *R.f. greyii* individuals from different areas of South Australia, including Pearson I., have been successful. Family

TABLE 1
Family data on GOT variation

| GOT phenotype of parents | Number of matings | Number and GOT phenotype of offspring | | |
|--------------------------|-------------------|---------------------------------------|----|---|
| | | A | AB | B |
| A x A | 2 | 3 | 0 | 0 |
| A x A [*] | 10 | 44 | 0 | 0 |
| A x B | 3 | 0 | 9 | 0 |
| A x AB | 1 | 2 | 0 | 0 |
| B x AB | 1 | 0 | 4 | 0 |

* One parent was not scored for GOT phenotype. However, in each of the ten matings it was known to have come from a population apparently monomorphic for the *Got-1^a* allele.

data on the inheritance of the GOT variation (Table 1) is consistent with a 1 locus, 2 allele mode of inheritance.

The *R.f. greyii* population on the northern section is monomorphic for the *Got-1^b* allele, while both *Got-1^a* and *Got-1^b* are present in the population on the southern and middle sections (Table 2). The genotypic frequencies in the latter population fit the Hardy-Weinberg equilibrium frequencies ($P > 0.05$). If the *Got-1^a* allele is present in the population on the northern section, then there is a 95% probability that its frequency is less than 3%. In any case, the frequency of the *Got-1^b* allele in the northern section is significantly different from its value in the middle and southern sections ($P < 0.001$).

TABLE 2
GOT phenotype distribution in animals caught on Pearson I.

| Area caught | Number and GOT phenotype | | | Frequency of <i>Got-1^b</i> |
|-----------------------------|--------------------------|----|----|---------------------------------------|
| | A | AB | B | |
| Northern section | 0 | 0 | 49 | 1.00 |
| Middle and southern section | 10 | 10 | 4 | 0.375 |

It seems unlikely that the marked difference in allelic frequencies is maintained by selection. All three sections of the island appear to provide very similar habitats for *R.f. greyii*. The observed absence of *Got-1^a* from the northern section indicates a severe restriction in gene flow between the areas sampled on the middle and northern sections. The most obvious point of demarcation is the channel separating the two sections. This surprisingly low level of migration between the northern and middle sections is similar to that found in the Pearson I. wallaby.

It would appear improbable that the rats are not physically capable of crossing the channel. When the sea is calm and the tide low, it is



Origin

Fig. 2. GOT variation found in *R.f. greyii* from Pearson I. The pattern of variation is in agreement with a dimeric molecule being the active enzyme.

easy for a man to wade or step from rock to rock between the two sections. However, the conformation of the channel is probably in a state of continual change. The relationship between sea level changes and the occurrence of one or more species of small macropod marsupials on small islands off the Western Australian coast has been discussed by Main (1961). From Main's data it appears that Pearson I. has been isolated from the mainland for at least 10,500 years. The northern and middle sections would have remained connected for a consid-

erable time after the isolation of the island. There is some evidence to suggest that since the isolation of Pearson Island from the mainland, the mean sea level on two or more occasions has been about 6 metres above its present level (Twidale, pers. comm.). During these times of high mean sea level, the channel would have been considerably larger than at present.

Thomas & Delroy (1971) suggested that the wallaby did not cross the channel because it found the sea water distasteful. Another possibility is that, because of the action of the sea, there may be strong selective pressures against small animals which wander too close to the edge of the water. Under such an hypothesis, genotypes would be favoured which predisposed animals to an aversion to moving close to the water's edge. This would discourage the animal from crossing between the middle and northern sections.

Various suggestions may be offered to account for the present distribution of the two alleles at the *Got-1* locus. All other populations of *R.f. greyii* studied (Greenly I., Hopkins I., Kangaroo I., Eyre Peninsula and Mount Lofty Ranges) have been found to be monomorphic for the *Got-1^a* allele (Schmitt, unpublished). The polymorphism on Pearson I. may have been present before the channel was formed and at that time, or some time afterwards, the *Got-1^a* allele was lost from the northern section. Alternatively, one of the alleles could have arisen by mutation, since the channel was formed. If the *Got-1^b* allele is the more recent mutant, then it has to be postulated that it subsequently migrated across the channel.

The channel separating the northern and middle sections has not only acted as an effective barrier to migration for the Pearson I. wallaby, but from the genetic evidence presented here, has also had a similar effect on *R.f. greyii*.

Thirteen other gene loci, for which about 70 specimens of *R.f. greyii* from Pearson I. have been scored, are monomorphic on Pearson Island and show no differences across the channel. However, all Pearson I. animals have haemoglobin and malate dehydrogenase proteins that are electrophoretically distinct from all other populations studied (Schmitt, unpublished).

Further studies on the situation described here would be a useful part of any future expeditions to Pearson I.

Acknowledgments

I wish to thank Dr D. L. Hayman, Dr R. M. Hope and Professor J. H. Bennett for their thoughtful discussion and help in the preparation of the manuscript. Transport to Pearson

Island was generously arranged by Mr M. Koch and provided by Mr R. Baker and Mr K. White. The South Australian National Parks and Wildlife Service granted a permit to allow me to collect specimens.

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TWO NEW SPECIES OF THE GENUS *CLOACINA* (NEMATODA: STRONGYLIDA) FROM THE TAMMAR, *MACROPUS EUGENII*

*BY PATRICIA M. MAWSON**

Summary

MAWSON, P. M. (1974).-Two new species of the nematode genus *Cloacina* (Nematoda: Strongylida) from the Tamar, *Macropus eugenii*. *Trans. R. Soc. S. Aust.* **99**(1), 39-41, 28 February, 1975.

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TWO NEW SPECIES OF THE GENUS *CLOACINA* (NEMATODA: STRONGYLIDA) FROM THE TAMMAR, *MACROPUS EUGENII*

by PATRICIA M. MAWSON*

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Introduction

The species which are described in this paper occur commonly and in considerable numbers in the stomach of the Tamar on Kangaroo Island. They were taken in the course of a quantitative analysis by Mrs Lesley Smales of the nematodes present at different times of the year in the stomach of this host, undertaken as part of work for a Ph.D. degree in the Department of Zoology.

Types of the new species will be deposited in the South Australian Museum; paratypes are in the Helminthological Collection of the Zoology Department, University of Adelaide.

Measurements of the two species are given in Table 1.

Cloacina smalesae n. sp.

FIGS 1–7

Host and Locality: *Macropus eugenii* (Desmarest), from Kangaroo I., S. Aust.

This is a medium-sized species of *Cloacina*, with markedly swollen cuticle at the anterior end. The thickness of the cuticle increases from the level of the posterior end of the oesophagus to the base of the mouth collar, which it surrounds like a platform. The mouth collar is well developed and slightly lobed anteriorly; it bears the four submedian cephalic papillae and two amphids. The distal segment of each cephalic papilla is longer and slightly thicker than the proximal segment. Each element of the leaf crown is domed anteriorly and is without the unguiform anterior projection usually present in species of this genus.

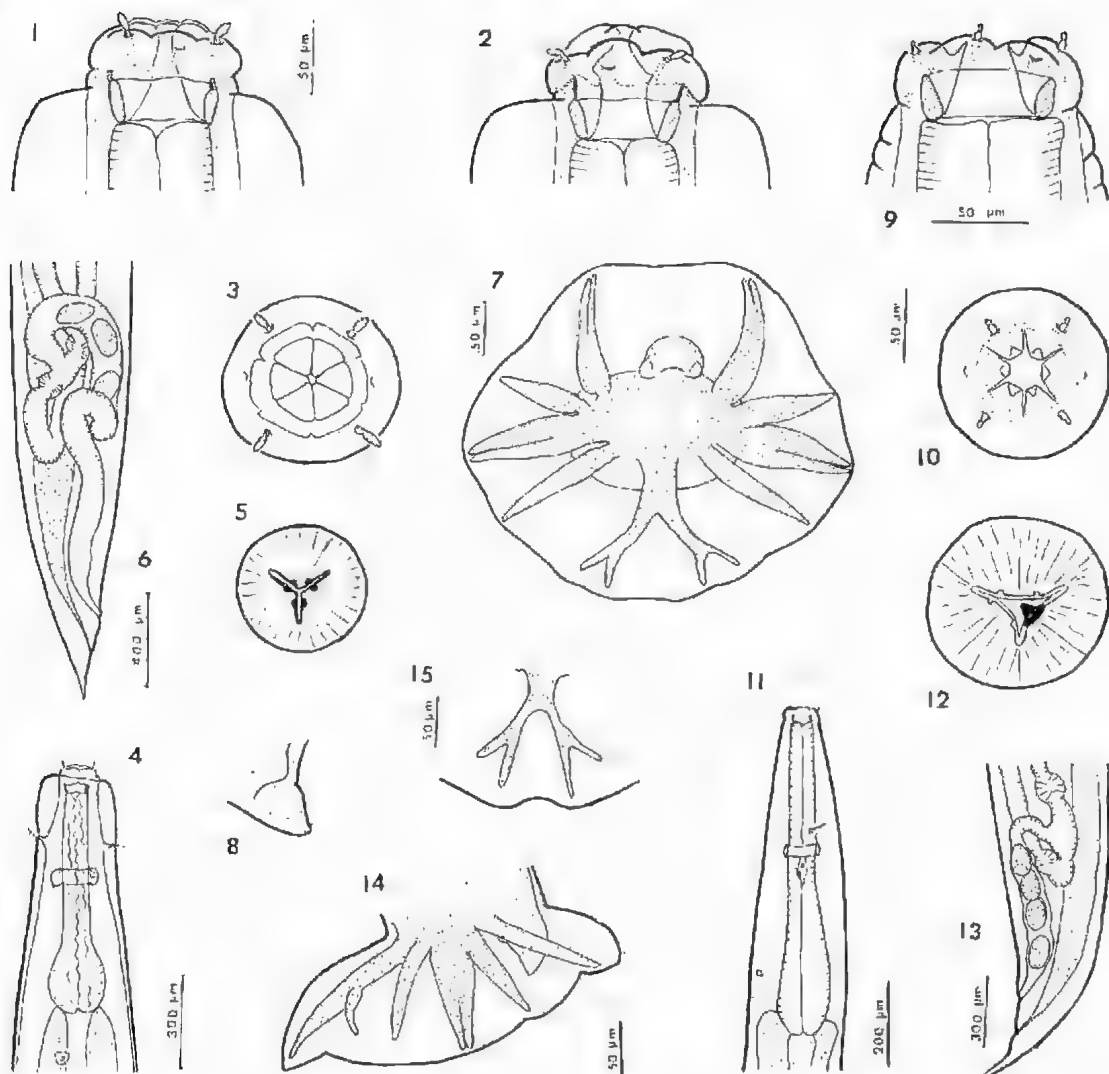
The buccal ring is circular and stoutly built. Its anterior and posterior walls are slightly lobed (Figs 1, 2). The oesophagus is cylindrical for most of its length, ending in a small swelling. There are no oesophageal teeth. The thickened lining of the lumen is unusually distinct, appearing in the whole mount as three wavy longitudinal lines throughout the length of the oesophagus. In transverse section the lumen appears triradiate with a thickening of the lining in the midlength of each arm. The nerve ring lies at about midlength of the oesophagus. The excretory pore is postoesophageal, and the cervical papillae lie a little distance in front of the nerve ring.

The bursal lobes are only slightly divided. The arrangement of the rays (Fig. 6) is typical for the genus. The genital cone is not prominent; it bears a small ala on each side of the cloaca, but no other appendages. The spicule is a little less than half the body length.

The tail of the female is conical, ending in a point. The vulva is slightly less than a tail length in front of the anus. The ovejectors unite 6–7 tail lengths in front of the vulva, and the vagina curves forwards before passing back, with one or two twists, to the vulva.

The rounded elements of the leaf crown seen in this species have been described in only one other species, *C. longilabiata* Johnston & Mawson, 1939b (syn: *C. minor* J. & M., nec. Davey & Wood, 1938). However, in *C. longilabiata* the vagina is shorter, the cephalic papillae are of a different shape and there is no cuticular inflation at the anterior end.

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Figs 1-8. *Clouvina smalesae*. Fig. 1.—Anterior end, lateral view. Fig. 2. Anterior end, showing leaf crown in everted position. Fig. 3.—Anterior end, *en face*. Fig. 4.—Oesophageal region. Fig. 5.—Transverse section of oesophagus, anterior to nerve ring. Fig. 6.—Posterior end of female. Fig. 7.—Bursa, flattened out and viewed from the inside. Fig. 8.—Lateral view of genital cone. Figs 1, 2, 3, 5 and 8 to same scale.

Figs 9-15. *Clouvina kartana*. Figs 9 and 10.—Sublateral and *en face* views of anterior end. Fig. 11.—Oesophageal region. Fig. 12.—Transverse section of oesophagus, showing one oesophageal tooth. Fig. 13.—Posterior end of female. Fig. 14.—Bursa. Fig. 15.—Dorsal ray. Figs 10 and 12 to same scale.

***Cloacina kartana* n. sp.**

FIGS 8-14

Host and Locality: *Macropus eugenii* (Desmarest), from Kangaroo I., S. Aust.

This is a medium-sized species of *Cloacina* with a well developed mouth collar bearing the four small submedium cephalic papillae and the amphids. The cephalic papillae are small;

the proximal segment is longer and slightly thicker than the distal one. The buccal ring is stoutly built, and is thicker posteriorly than anteriorly. The six elements of the leaf crown do not, in the resting position at least, project above the collar.

The oesophagus is cylindrical for most of its length, with a terminal bulb. There are two small subventral oesophageal teeth, one a little

TABLE 1

Measurements of Cloacina smalesae and C. kartana; in μ m unless otherwise stated.

| | <i>C. smalesae</i> | | <i>C. kartana</i> | |
|----------------------|--------------------|---------------|-------------------|---------------|
| | ♂ | ♀ | ♂ | ♀ |
| Length (mm) | 9.5-11.4 | 13.0-15.8 | 8.0-10.9 | 12.4-17.0 |
| Oesophagus | 690-720 | 710-790 | 680-790 | 810-900 |
| Antr. end—nerve ring | 360-400 | 360-490 | 300-350 | 340-400 |
| —cerv. pap. | 200-230 | 160-200 | 220-300 | 250-300 |
| —excr. pore | 790-870 | 910-1000 | 600-740 | 700-800 |
| Spicule length | 4200-4700 | — | 1400-1600 | — |
| Length/spic. l. | 2.2-2.5 | — | 5.7-7.1 | — |
| Length/oesoph. | 13.8-16.0 | 16.8-21.8 | 10.6-16.0 | 14.3-20.9 |
| Tail | — | 220-260 | — | 200-300 |
| Postr.—vulva | — | 350-490 | — | 380-500 |
| Egg length x breadth | — | 170-175x85-90 | — | 180-185x85-90 |

posterior to the other, at about midlength of the oesophagus, and shortly behind the nerve ring. The cervical papillae lie just in front of the nerve ring, and the excretory pore is at the level of the oesophageal bulb.

The spicules are relatively short. The lobes of the bursa are distinct but not deeply separated. The rays are arranged as shown in Figs 13 and 14. The genital cone is small and no appendages were seen on it.

The female tail is conical, ending in a narrowed point. The vulva lies a little less than

a tail length in front of the anus; the vagina, which is straight, extends about 3-4 tail lengths in front of the vulva.

The species most closely resembles *C. obtusa* Johnson & Mawson, 1939a, but differs in the spicule length.

Acknowledgments

My thanks are due to Mrs. Smales for the collection of the specimens described. Part of the work was done under a Grant from the Rural Credits Development Fund.

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**THE GENERAL WATER CIRCULATION OF SPENCER GULF,
SOUTH AUSTRALIA,
IN THE PERIOD FEBRUARY TO MAY**

*BY D. A. BULLOCK**

Summary

BULLOCK, D. A. (1975). -The general water circulation of Spencer Gulf, South Australia, in the period February to May. *Trans. R. Soc. S. Aust.* **99**(1), 43-53, 28 February, 1975.

Historical temperature and salinity data are presented together with the three-dimensional velocity structure of the general water circulation of Spencer Gulf, deduced from the data using a numerical model. In the southern area of the Gulf a cyclonic gyre is found which exchanges Gulf water with the ocean water outside the Gulf. On the western coast of the Gulf, a moderate boundary flow, which is called the "Port Lincoln Boundary Current", is evident at all depths. The water in the northern portion of the Gulf circulates both in the vertical and the horizontal and appears to form an almost closed system separate from the system in the southern region.

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Introduction

An investigation of the general water circulation in Spencer Gulf, and the region outside it, is made below from observation of property distributions and using a numerical model. The term "general water circulation" is used so that tidal currents which basically involve a periodic north-south movement of the Gulf's waters are excluded. Tidal currents can be superimposed on the more sustained flows caused by thermohaline (and wind) forcing which are particularly important because of the part they play in the interchange of water in a substantially enclosed body of water. Thermohaline currents are brought about by horizontal pressure gradients due to density variations in the Gulf, which are caused by temperature and salinity differences, produced in part by outside water entering the Gulf, and in part by variation in the effect of evaporation over the Gulf.

All available data for the region, obtained on C.S.I.R.O. cruises, are shown in Fig. 1. The cruises took place between 1961 and 1966 during the months indicated in the caption. No direct current readings are available, although some results on surface drift do exist from a drift card experiment. (Marshall & Radok 1972).

Presentation and Interpretation of Cruise Data

Using measurements made by F.R.V. Investigator (C.S.I.R.O. Aust., 1968c) on 7 May 1964, a vertical salinity section (Fig. 2a) was drawn for a line across the mouth of Spencer Gulf from Port Lincoln on the western side to Corny Point on Yorke Peninsula. The salinity is approximately homogeneously distributed over depth for any particular water column, although around the centre the situation is closer to that of a two-layer system since the salinity is almost constant with depth until about 20 m, at which point a steep salinity gradient occurs. Below this, the salinity is again constant with depth but greater than before. Also, the salinity increases with distance from west to east, indicating that water enters the Gulf on the western side and leaves via the eastern side after its salinity has increased due to evaporation and mixing. The density section (Fig. 2b) has a similar form to the salinity section, indicating that salinity is the dominant factor in determining thermohaline flow.

The most important feature of the hydrology of Spencer Gulf, evident from all data (Figs 10, 11), is that the water is approximately homogeneous from top to bottom, and hence

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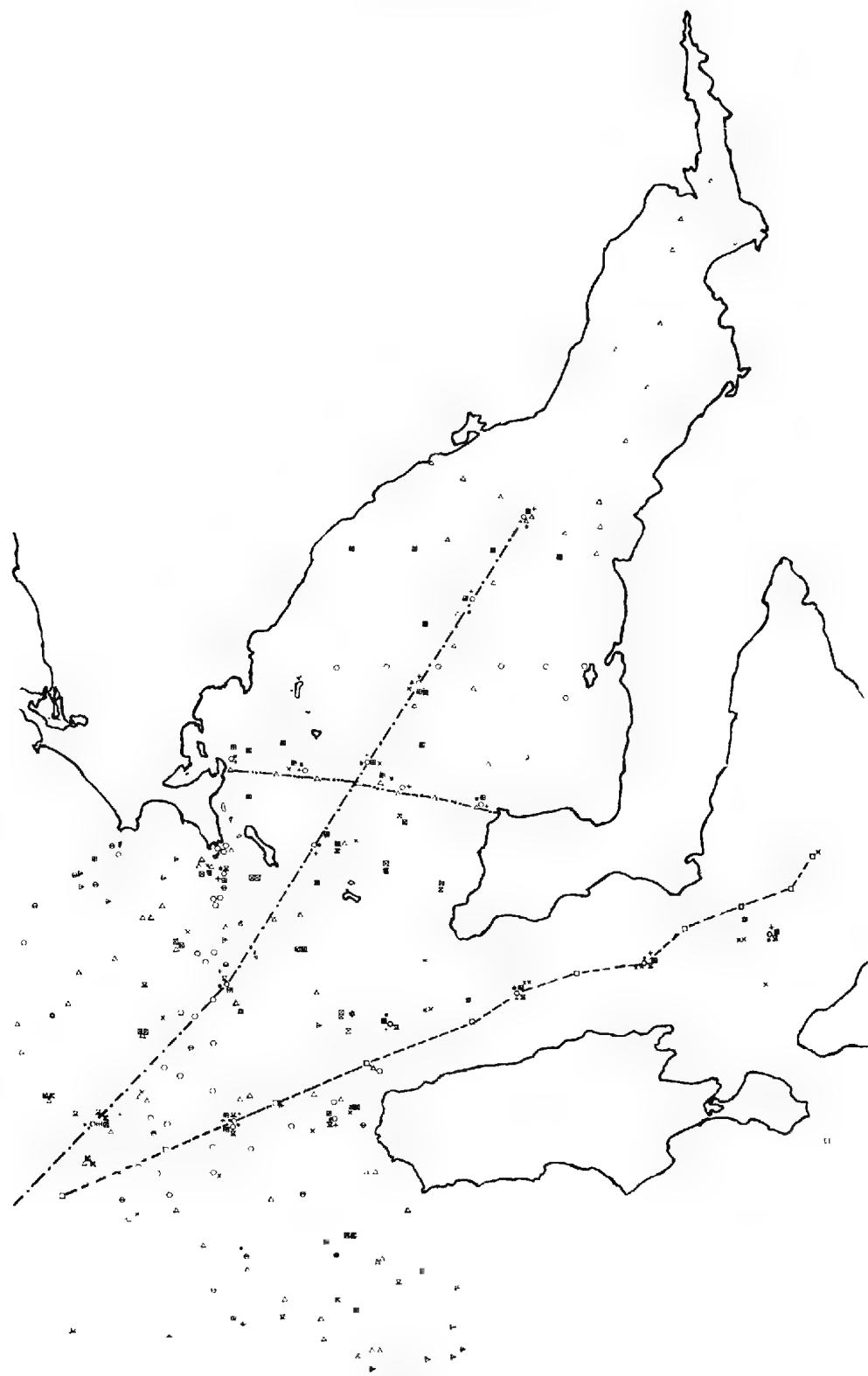


Fig. 1.

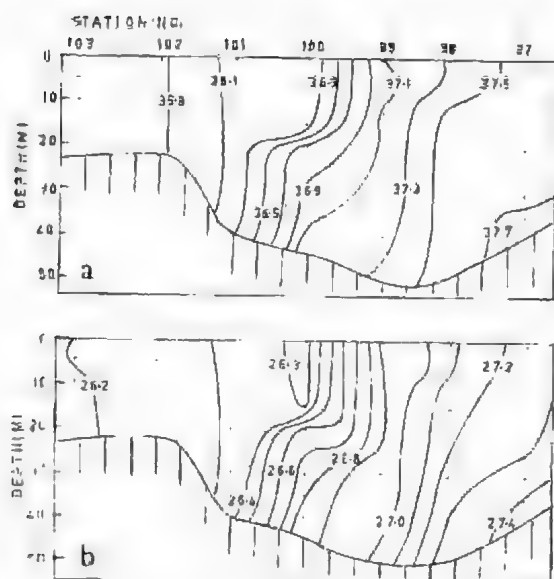


Fig. 2. Vertical sections across Spencer Gulf near the mouth, Marked — on Figure 1, data taken from CSIRO Aust. 1968, sampling depths indicated by dots.
(a) Salinity (‰), (b) σ_t .

it is reasonable that the quantities be represented by their depth-average. Fig. 3a-c shows horizontal depth-average distributions of salinity, temperature and density drawn from data obtained in the period 4-7 May 1964 (C.S.I.R.O. Aust. 1968c). Although other measurements have been made in Spencer Gulf, this cruise was by far the most comprehensive. From experience it was found necessary to restrict the data used to that obtained on one cruise, which spans only a short duration, so that seasonal and shorter term variations in properties do not cause misleading interpretations to be made.

The distributions shown in Fig. 3 are consistent with those in Fig. 2 and give additional information. A flow up the western shore is evident and it can be seen that the salinity increases eastward over the whole southern area of the Gulf indicating that the movement of water is basically clockwise. It appears that the advective exchange with the water outside the Gulf is limited to the area below a latitude of about 33°45'S. Above this region where the Gulf narrows, the water appears "blocked-in". Along the eastern and central areas of the upper part of the Gulf, the high salinity water seems to flow down the Gulf until it meets the lower salinity water taking part in the advective process described above.

The data from the northern part indicate that the water moves as a mass in phase with the tidal currents. At 34°00'S, 137°10'E, two stations (76 and 89) were occupied, separated by a period of 29 hours during which the depth-average salinity changed from 38.40‰ to 38.14‰. At 33°57'S, 137°25'E (stations 77 and 85), the salinities changed from 38.35‰ to 38.60‰ over a period of 21 hours. Using the horizontal salinity gradients at this location, Fig. 3 shows that this salinity variation corresponds to a tidal excursion of a few kilometres.

The mechanism responsible for the homogeneity of the water columns is based on vertical mixing promoted by tidal currents, which are amplified by the shallow water, running over a rough bottom which enhances vertical diffusion by the shear effect (Bowden 1965).

The temperature variation over the Gulf is small (Fig. 3b); a plausible explanation for this observation is the following. Since, in the north of the Gulf, the advective exchange of properties is small and the water shallow, the effects of evaporation are more marked than further south, as is reflected by the high salini-

Fig. 1. Location of Oceanographic Stations in the South Australian Gulf System until 1973.

Key to Symbols

- H.M.A.S. Gascoyne (G2/61) Feb.-March 1961 (CSIRO Aust. 1966)
- H.M.A.S. Gascoyne (G2/63) March 1963 (CSIRO Aust. 1967a)
- ◻ H.M.A.S. Gascoyne (G5/65) March-April 1965 (CSIRO 1967b)
- H.M.A.S. Gascoyne (G2/62) June-Aug. 1962 (CSIRO Aust. 1967c)
- ▨ H.M.A.S. Gascoyne (G2/64) Feb. 1964 (CSIRO Aust. 1967d)
- ▩ H.M.A.S. Gascoyne (G2/65) Feb. 1965 (CSIRO Aust. 1968a)
- ✦ H.M.A.S. Diamantina (Dm2/66) April 1966 (CSIRO Aust. 1969)
- F.R.V. Investigator 1963 (CSIRO Aust. 1968b)
- ◐ F.R.V. Investigator 1964 (CSIRO Aust. 1968c)
- ◑ F.R.V. Investigator Dec. 1962 (CSIRO Aust. 1968d)
- ▨ F.R.V. Investigator Feb. 1965 (CSIRO Aust. 1968e)
- ▩ F.V. Estelle Star April-May 1965 (CSIRO Aust. 1968f)
- F.V. Estelle Star April 1966 (CSIRO Aust. 1968g)
- F.R.V. Weerutta Jan.-March 1961 (CSIRO Aust. 1968h)

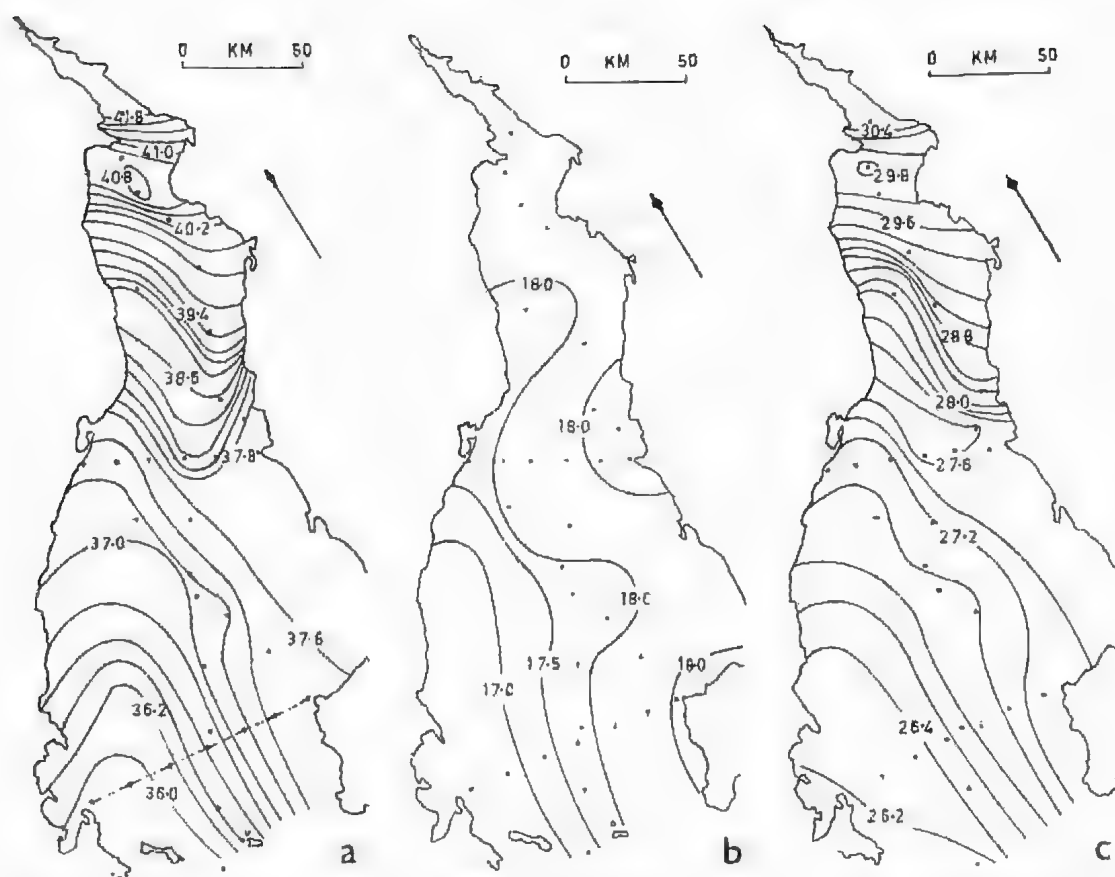


Fig. 3. Horizontal depth-average distributions in Spencer Gulf. Data taken from CSIRO Aust. 1968c. (a) Salinity (‰), (b) Temperature (°C), (c) σ_t .

ties. The process of evaporation requires the extraction of latent heat of vaporisation which in turn lowers the temperature and nullifies the effect of direct heating. The following rough calculation shows that there is an approximate balance between the heat input from the atmosphere and the heat output due to evaporation. From Haney (1972), the heat flux/unit area is proportional to the difference between the apparent air temperature and the sea temperature (denoted by T_a^* and T_s respectively). Assuming this flux is all available for evaporation, we obtain

$$E = \lambda(T_a^* - T_s)$$

where E is the evaporative heat flux/unit area, and approximately $\lambda = 34 \text{ Wm}^{-2}(\text{°C})^{-1}$ (Haney 1972). Taking the values, $T_a^* = 21\text{°C}$ (the mean temperature for early April), and $E = 100 \text{ Wm}^{-2}$, and substituting in equation (1) yields $T_s = 18\text{°C}$, which is approximately the

observed value (Fig. 3b). The neglect of advective exchange is justifiable in view of the observed small variation of temperature and closed nature of the circulation in the northern Gulf. Vertical mixing maintains the temperature difference between the atmosphere and the sea surface.

Locations of the stations are shown by the dots in Fig. 3a-c; stations were not occupied in some areas, notably above Hardwick Bay on the eastern side of the Gulf. Nevertheless, the overall pattern of water properties can be inferred reasonably accurately.

The Numerical Model

In order to investigate whether the above circulation could be considered as primarily due to thermohaline forcing or whether some other cause such as wind is dominant, and discover in greater detail the dynamics of Spencer Gulf, a numerical model was used to derive theoretic

tically the field of flow from the density field shown in Fig. 3c. The model entitled FLOWDEN computes the currents generated in a sea of density independent of depth, by wind and variations in atmospheric pressure, and by the

horizontal pressure gradients induced by the density field¹. This is done by solving the finite difference representation of the component transport equations written in a form applicable to the terrestrial situation².

$$\frac{\partial U}{\partial t} = fV - gH \frac{\partial \eta}{\partial x} - g^* \frac{H^2}{2} \frac{\partial \sigma_t}{\partial x} + \frac{\tau_{sx}}{\rho_0} - K|u_B|u_B \quad (2)$$

$$\frac{\partial V}{\partial t} = -fU - gH \frac{\partial \eta}{\partial y} - g^* \frac{H^2}{2} \frac{\partial \sigma_t}{\partial y} + \frac{\tau_{sy}}{\rho_0} - K|v_B|v_B \quad (3)$$

where the following notation is used;

$$U = \int_{-H}^{\eta} u dz, \quad V = \int_{-H}^{\eta} v dz$$

u = eastward component of velocity (east $\equiv x$ direction)

v = northward component of velocity (north $\equiv y$ direction)

u_B, v_B = x & y components of bottom velocity (u_B)

z = distance measured perpendicular to earth's surface, positive upwards

σ_t = $(\rho - 1) \times 10^{-1}$, ρ in kg l^{-1}

f = Coriolis parameter = $2\omega \cos \phi$, ω = angular speed of the earth's rotation, ϕ = latitude

H = depth

$g^* = 10^{-3} \alpha_{35,0,0} g$, $\alpha_{35,0,0}$ = specific volume of the standard ocean

g = gravitational acceleration

η = sea surface elevation

K = bottom drag coefficient

ρ_0 = density of a standard ocean = $\frac{1}{\alpha_{35,0,0}}$

τ_{sx}, τ_{sy} = x & y components of surface wind stress

The terms in equations (2) and (3) have the following physical meanings: the left-hand sides are the linearized accelerations, the first terms on the right-hand sides are the Coriolis accelerations, the second terms are the horizontal pressure gradients due to elevation of the surface, the third terms are the thermohaline terms which take into account the horizontal pressure gradients due to the inhomogeneity of the horizontal salinity and temperature distributions. The final two terms are stress terms describing wind and bottom friction respectively.

The magnitudes of the thermohaline terms were evaluated using another computer programme from the observed density distribution (Fig. 3c) and the depths were interpolated from those given on a naval hydrographic chart. A typical value of the x component of

the thermohaline terms was $300 \text{ mm}^2 \text{ s}^{-2}$. This can be compared with the typical magnitude of $100 \text{ mm}^2 \text{ s}^{-2}$ for the forcing term corresponding to wind stress, so that the circulation in Spencer Gulf due to thermohaline causes can be expected to be quite significant. The bottom drag coefficient $K = .0025$.

FLOWDEN was run with the precalculated thermohaline term as the only forcing term and with the thermohaline term together with a constant wind. After the equivalent of 17 hours an equilibrium current was reached (actually a small oscillation about the solution remained, but this was ignored). The initial conditions were that the flow velocity was zero everywhere and the surface elevation was also zero everywhere except at the boundary of the model across the south of the Gulf, which was assumed to have an initial slope similar to that

¹ Bye, J. A. T., 1975. Thalasso-scale numerical modelling. Computer Report. School of Earth Sciences. The Flinders University of South Australia. (Unpublished.)

² Bullock, D. A. 1973. The general circulation of St. Vincent and Spencer Gulf. Honours Thesis, The Flinders University of South Australia. (Unpublished.)

developed later in the adjacent part of the Gulf. The boundary slope was found to have little effect on the current distribution and so the assumption is presumed to not have serious consequences.

The resultant depth-average current, which is the transport divided by the depth, was obtained at each point of a grid system formed over the Gulf, in polar form so that the magnitude and direction of the current could be seen immediately. The grid length was 6.4 km.

$$u(z) = \frac{U}{H} + \frac{g^*}{f} \frac{\partial \sigma_t}{\partial y} \left(z + \frac{H}{2} \right) \quad (4)$$

$$v(z) = \frac{V}{H} - \frac{g^*}{f} \frac{\partial \sigma_t}{\partial x} \left(z + \frac{H}{2} \right) \quad (5)$$

Applying equations (4) and (5) at $z = \tau \approx 0$ and at $z = -H$ gives the surface and bottom currents.

Since σ_t is independent of z it can be seen from equations (4) and (5) that the vertical homogeneity of the Gulf implies that the current is a linear function of depth z . Thus a shear current exists. The right-hand side of equation (4) and (5) can be interpreted as follows. The second terms are symmetric about a line marking mid-depth (Fig. 4) and give, as a function of depth, the current which is directly related to the local distribution of density. The first terms on the right-hand side of the equations, on the other hand, represent the depth-average current predicted by the model under the constraints imposed by the boundaries of the Gulf (the shores and bed).

The vertical components of velocity were also found, using the bottom current and the gradients of the bottom topography,

$$w = u_B \frac{\partial H}{\partial x} + v_B \frac{\partial H}{\partial y} \quad (6)$$

Finally, the changes in the sea level which develop from the initial surface condition of zero slope are also obtained.

Results of the Numerical Model

(1) Predicted Velocity Fields due to Thermohaline forcing only

Fig. 5 shows the main features of the predicted depth-average current. The figure is consistent with the water mass analysis of the previous section, i.e. the circulation in the wide, southern part of Spencer Gulf consists of a clockwise gyre, water entering via the western side and leaving on the eastern side and the circulation in the northern end appears closed.

To gain a detailed picture of the velocity field in the Gulf, a routine was added to the program which printed out the surface and bottom currents. By involving the shallow water assumption, i.e. that the Ekman layer (the surface layer influenced by wind) and the layer of bottom frictional influence overlap (an assumption which is consistent with the waters' vertical homogeneity), it can be shown (Bullock 1973—footnote 2) that the current components at any level are given by,

The magnitude of the velocity vectors shown is typically about 0.07 ms^{-1} (ranging from zero to 0.15 ms^{-1}).

From Figs 6 and 7, which show the surface and bottom currents respectively, it can be seen that at both the surface and bottom there is a very distinctive flow up the western side of the Gulf, which we shall call the "Port Lincoln Boundary Current". This current is broader in extent at the surface than at the bottom where it tends to peel away to the east down the slope of the bottom. The Port Lincoln Boundary Current is also somewhat stronger at the surface than at the bottom due to the frictional influence of the latter.

The direction of the bottom current can be seen to swing eastward and then to the south-east over a broad area before flowing southward to exit down the shovel-shaped topography through the Gulf's mouth. The surface current displays a similar pattern; however, since the Port Lincoln Boundary Current is wider at the surface, particularly near the mouth, the centre of the gyre of the surface circulation is located further to the north-east than the centre of the bottom gyre. Evidence of the eastward movement of water from the boundary current is also provided by Fig. 3a-c where the contours bulge to the east in this area.

The differences between the top and bottom current gyres implies that the surface and bottom currents on the eastern side of the Gulf are, in general, at an angle to each other, unlike the western boundary. This explains why there is no obvious salinity or σ_t tongue indicating a return flow down the eastern side of the Gulf in Fig. 3b and c.

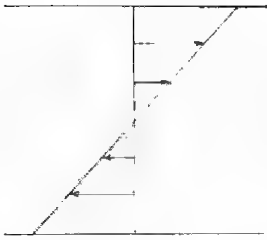


Fig. 4. Current as a function of depth, with reference to mid-depth.

Another important feature to be noted from Figs 6 and 7 is that in the centre of the mouth the surface and bottom currents are in opposite directions so that a large shear is predicted here. The closeness of the density and salinity sections (Fig. 2b and 2a) to those of a two-layer system is also explained by this phenomenon. It would be interesting to make direct current measurements in this area.

Further north, where the Gulf starts to narrow (at about the latitude of Wallaroo), the flow pattern is more complicated and conver-

gences of the currents exist. A large proportion of the water in the northern end appears to recirculate in a vertical gyre. Fig. 8, which shows the vertical components of velocity, lends support to this interpretation by the downwelling at the top of the Gulf near Point Lowly, which corresponds to an inflexion in the salinity contours (Fig. 3a). In the southern part of the Gulf, a complex system of vertical cells of typical dimension 20 km is predicted.

The following changes in surface elevation are predicted by the model: in the southern part of the Gulf, a low develops, the sea level on the western side being between 10 and 50 mm higher than in the centre; the sea level also increases to the north. We can conclude that the circulation in Spencer Gulf which can be attributed solely to thermohaline causes is of significant magnitude and forms a major contribution to the water exchange processes of the Gulf.

(2) *Velocity field due to Thermohaline and Wind Forcing*

The numerical experiment was now extended to include the effect of wind stress in addition

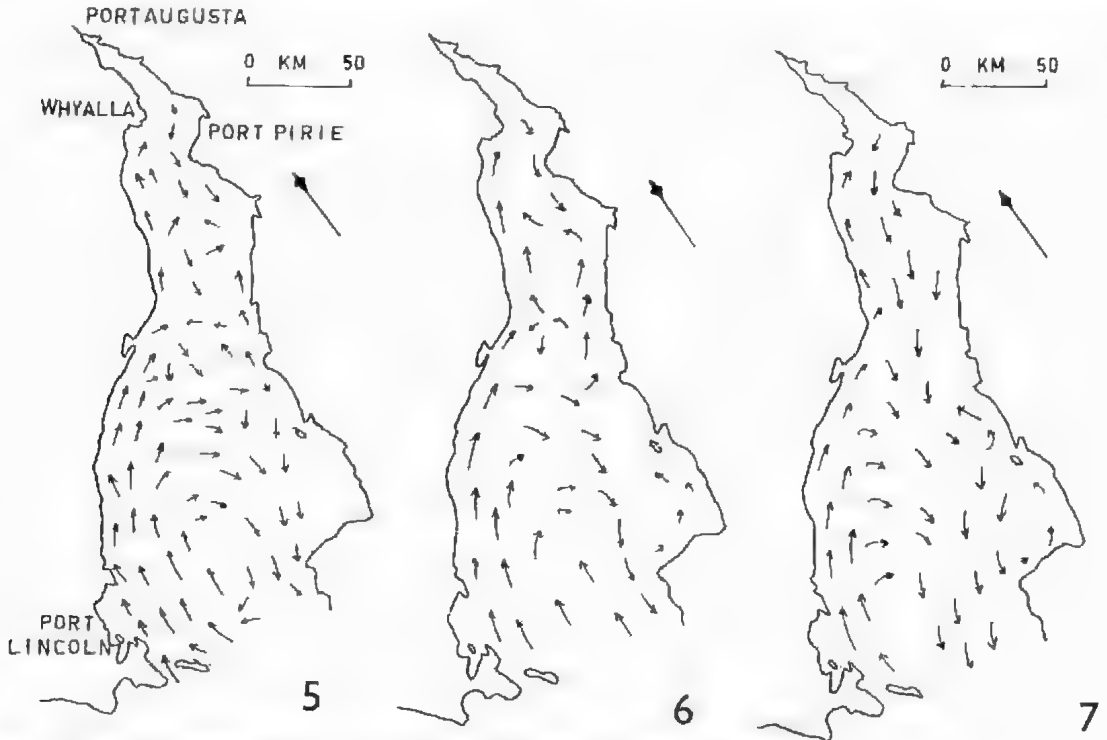


Fig. 5. Predicted depth-average thermohaline currents in Spencer Gulf.

Fig. 6. Predicted surface thermohaline currents in Spencer Gulf.

Fig. 7. Predicted bottom thermohaline currents in Spencer Gulf.

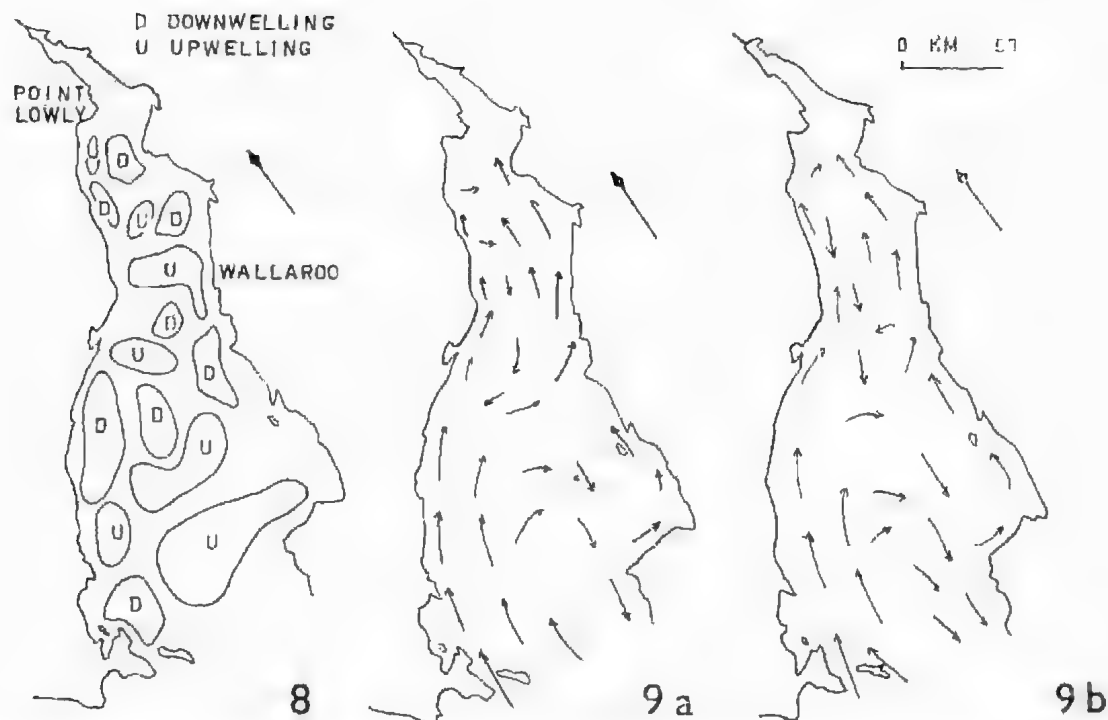


Fig. 8. Predicted regions of up- and down-welling due to thermohaline currents in Spencer Gulf.
 Fig. 9. Predicted currents in the presence of a 14 ms^{-1} SW wind.
 (a) Surface, (b) Bottom.

to the thermohaline forcing. The resulting surface and bottom currents predicted by the model for the same density structure as before, combined with a 14 ms^{-1} south-west wind, are shown in Fig. 9a and 9b.

The pattern of circulation is basically the same but the velocity of the flow is accentuated, being typically about 0.16 ms^{-1} , some velocity vectors having a magnitude over 0.30 ms^{-1} . Differences to the no-wind case do occur in the northern part of the Gulf where the surface current is predominantly northward in direction, particularly on the eastern side where it was directed southwards previously. Similarly the bottom current flows north adjacent to the shores, whereas in the no-wind case the bottom current was slight here. It can also be seen that with the wind added, the surface and bottom currents are almost the same everywhere.

The model predicts that the surface elevation increases greatly (up to 0.37 m) with distance up the Gulf, i.e. the water is piled up at the northern end by the wind. The low in the southern half is also accentuated, the level being raised by up to 80 mm around the shores

compared with the depression of 10 mm in the centre.

(3) Possible reasons for the Persistence of the Density Structure

In the numerical model, the thermohaline forcing terms remained constant throughout the period from zero velocity to equilibrium; i.e. we assume that the observed density field persists and is not an instantaneous feature which subsequently runs down until the Gulf becomes a completely homogeneous body of water in which water motion of thermohaline origin would cease.

It is surmised that the cause of the persistence of the thermohaline circulation is external, i.e. it is due to water from the Southern Ocean moving up under influences that determine the pattern of flow in this region, perhaps the prevailing westerly winds. Fig. 12, which shows the dynamic topography of the ocean south of Australia (Bye 1971), indicates that the direction of the geostrophic flow in the deep ocean is, in fact, basically perpendicular to the Australian coastline.

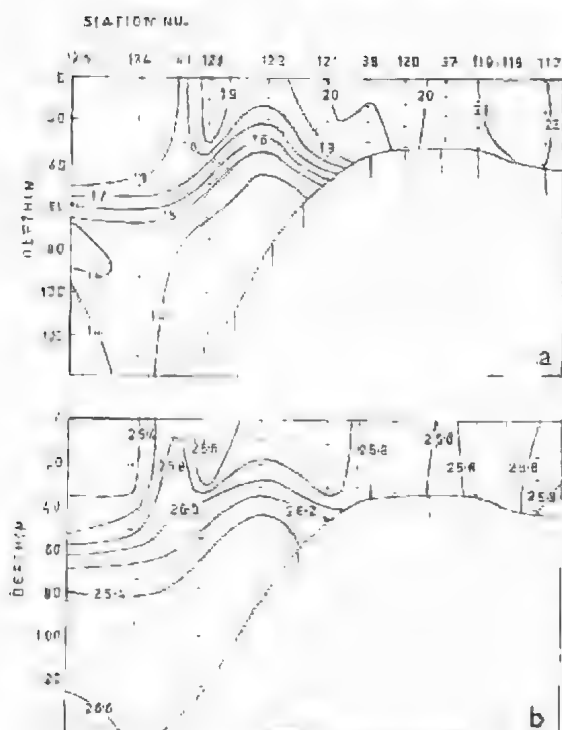


Fig. 10. Vertical sections along Investigator Strait to the Continental Slope. Marked --- on Figure 1, data taken from CSIRO Aust. 1966 and 1967a. Sampling depths indicated by dots.
(a) Temperature ($^{\circ}\text{C}$), (b) σ_t .

The other factor which exerts a continuous effect on Spencer Gulf is evaporation, which has the effect of maintaining a high salinity and hence a high density at the northern end. It is worth noting that in Fig. 3a the salinity tongue extending downward from the Gulf's northern end occurs over a favourable bottom gradient, whereas this is not so for the tongue which corresponds to the Port Lincoln Boundary Current.

(4) The Region Outside Spencer Gulf

The locations of measurements made in the area outside Spencer Gulf are shown in Fig. 1. Data from this region were obtained primarily to aid the fishing industry and suffer from the drawback that there are no synoptic surveys of the whole area, which would enable horizontal distributions of properties to be drawn. Only vertical sections and profiles can be satisfactorily constructed. The paths along which sections have been drawn are shown by the various lines in Fig. 1.

Fig. 10a and b show temperature and σ_t sections drawn along a line extending through Investigator Strait to past the end of the Continental Slope. The data were obtained in Feb.-March 1961 (C.S.I.R.O. Aust. 1966) and March 1963 (C.S.I.R.O. Aust. 1967a). One feature which is noticeable is the change in pattern from a vertically homogeneous situation just inside the mouth of Investigator Strait to the more complicated horizontal stratification in the deeper waters outside the Gulf.

The most significant feature shown by these sections, however, is the gradient in salinity, temperature and density about Station 122, which was located north-east of Cape Borda on the north-west tip of Kangaroo Island. This density gradient implies the existence of a thermohaline current, water to the west of Station 122 flowing approximately perpendicular to the plane of the section (into the page). This direction correlates very closely with the direction of the thermohaline current entering Spencer Gulf which forms the Port Lincoln Boundary Current. Conversely there is also a southward directed flow between Stations 121 and 122 which could have its origins in the outflow from the eastern side of Spencer Gulf. It is possible that upwelling is also occurring near the longitude of Station 122. The peak in the density lines for the surface water under Station 41 is explained by the fact that this station was occupied in a different year to the adjacent stations (although at the same time of the year), so that the surface water temperatures are not consistent.

The section shown in Fig. 11a and b runs roughly in a north-east direction from the Continental Shelf up Spencer Gulf (C.S.I.R.O. Aust. 1967a). The gradient of the lines adjacent to the rapidly deepening region outside Spencer Gulf under Station 64 again indicates a current inwards across the plane of the section, probably angled up slope so that the water inundates the more level sea bottom of Spencer Gulf. This is again in agreement with the previously deduced direction of flow into Spencer Gulf which is NNW and thus crosses the line of the section.

Fig. 12 shows that the direction of the circulation in the Southern Ocean is consistent with the flow in the region outside the Gulf as deduced from Figs 10 and 11.

Conclusion

The various data presented were mainly collected in the months of February to May,

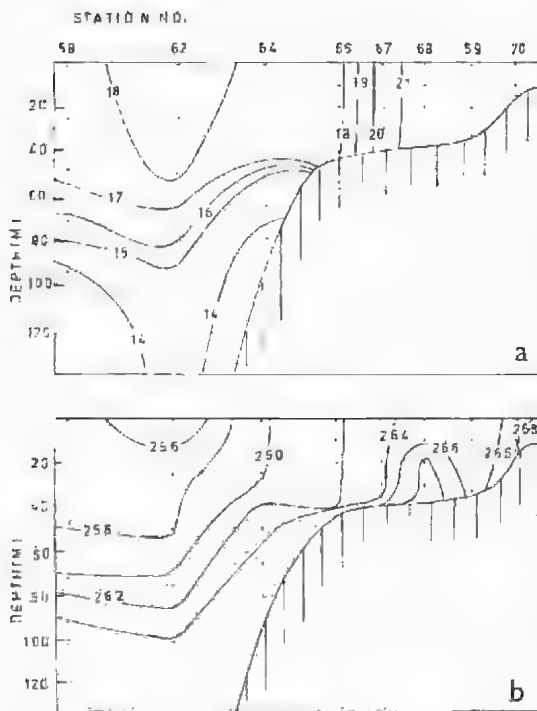


Fig. 11. Vertical sections along Spencer Gulf to the Continental Shelf. Marked — on Figure 1, data taken from CSIRO Aust. 1967a. Sampling depths indicated by dots.
(a) Temperature ($^{\circ}\text{C}$), (b) σ_t .

although during different years, so that it would appear that the general circulation deduced occurs at least seasonally. However, to gain a complete and detailed picture of the circulation in the Gulf, it is obviously necessary to conduct a series of thorough cruises at various times throughout the year. In addition, direct current measurements need to be made to check the results from the model. Since the dis-

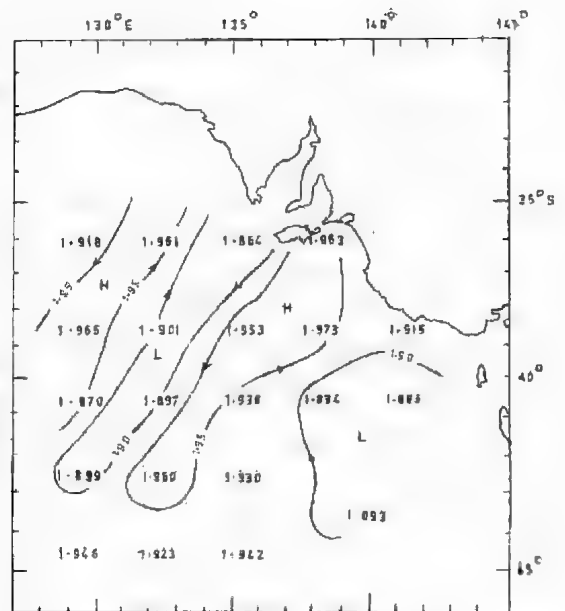


Fig. 12. Dynamic topography relative to 2000 db., south of Australia (taken from Bye 1971).

tributions of water properties in St Vincent Gulf have been found (Bullock 1974) to be similar to those in Spencer Gulf, it may be expected that the general circulation in St Vincent Gulf would also display a pattern basically similar to that in Spencer Gulf.

Acknowledgement

I am most grateful to Dr J. A. T. Bye for his guidance and advice during this study. Part of this material was presented at the Second South Australian Regional Conference on Physical Oceanography, University of Adelaide, 9 August 1973.

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A NEW PROCEDURE FOR MOUNTING CLEARED LEAVES USING POLYESTER RESIN

BY D. C. CHRISTOPHEL* AND D. T. BLACKBURN*

Summary

CHRISTOPHEL, D. C., & BLACKBURN, D. T. (1975).-A new procedure for mounting cleared leaves using polyester resin. *Trans. R. Soc. S. Aust.* **99**(2), 55-58, 31 May, 1975.

Palaeobotanical studies of leaf floras require detailed comparisons with extant leaves. Techniques for clearing and mounting extant leaves using either sodium or potassium hydroxide or a lacto-phenol solution as a clearing agent have long been known. This paper presents modification of this technique using an hydroxide clearing agent and mounting in polyester resin.

In this procedure leaves are cleared in 15% KOH followed by saturated chloral hydrate. Leaves are then dehydrated, stained with safranin and mounted in Mulford EX-80 polyester resin. Use of this mountant shortens preparation time by several weeks as well as giving superior transparency to specimens. Photographic reproduction using direct printing of specimens placed in an enlarger is also discussed.

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Introduction

The vast majority of plant macrofossils collected from Tertiary localities is in the form of compressed or impressed leaves. Identification of these leaves is made difficult by the fact that most extant correlatives are described and identified on the basis of floral parts. To overcome this problem, some palaeobotanists are now studying extant plants in terms of their "leaf architecture" (Hickey 1973). For this type of study, detailed observation of the higher order veins of angiospermous leaves is essential, and many workers (Chandrasekharam 1972¹, Christophel 1973², Hickey 1973) have found it advantageous to develop or modify techniques for clearing these leaves.

Of the many techniques developed to cope with this problem (Lersten 1967, Dilcher 1974), most can be divided into two broad categories. The first may be termed the lacto-phenol category, the most recent refinement of which has been presented by Herr (1972). This technique is characterized by rapid clearing (1-5 days) and by preservation of cellular and cuticular detail. Its disadvantages include inapplicability to some leaf forms (e.g. those with extremely tough cuticles or those

which are highly tomentose), and extreme difficulty in conversion to a permanent mount.

The second category of techniques, which may be collectively termed the hydroxide category, was used initially for the study of cauline vascular tissue (Foster 1952). It usually combines either sodium or potassium hydroxide treatment with further bathing in chloral hydrate or other bleaching agents. This method is characterized by its relatively long clearing time (four to ten weeks) and frequent loss of cellular and cuticular detail. It has the definite advantages, however, of working on almost all leaf types (given appropriate time) and of being readily combined with many permanent mounting techniques.

The technique presented in this paper is a modification of the hydroxide method. The major drawback of the technique in the past has been the large amount of time needed for the preparations. For example, to prepare a large leaf of *Cinnamomum* takes approximately four weeks in hydroxide, three days in chloral hydrate, one day for staining, and an additional three weeks for mounting and drying. This gives a total time of up to 54 days

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¹ Chandrasekharam, A. (1972).—Megafossil Flora of Genesee, Alberta. Ph.D. thesis, University of Alberta, Canada (unpublished).

² Christophel, D. C. (1973).—Fossil floras of the Smoky Tower locality, Alberta. Ph.D. thesis, University of Alberta, Canada (unpublished).

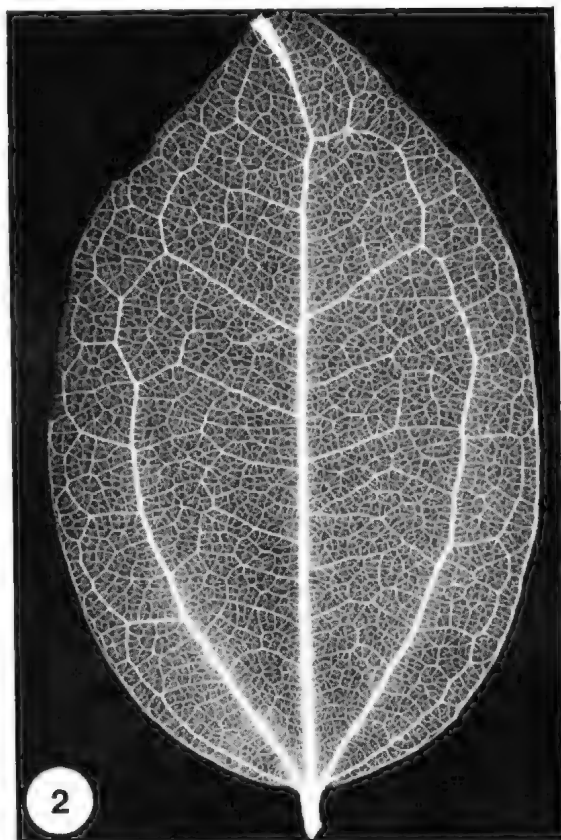
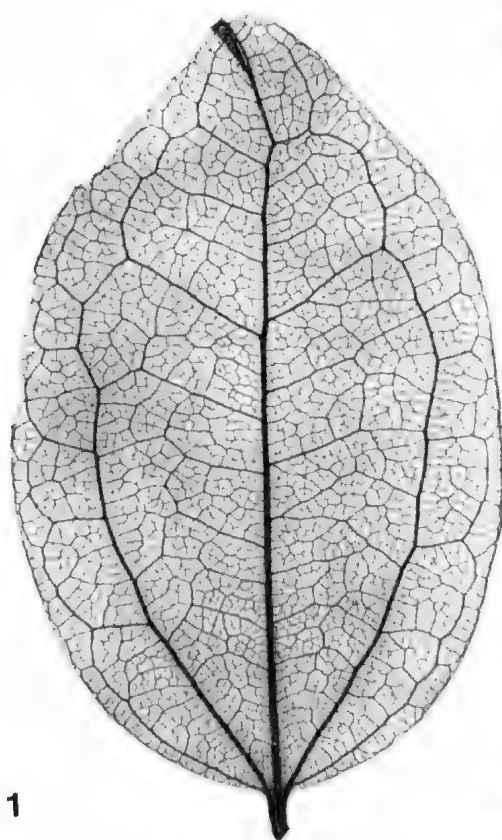


Fig. 1. *Strychnos lucida*—leaf cleared by potassium hydroxide-chloral hydrate method. Photographed with a Leitz Aristophot 4 x 5 plate camera. x 2.5.

Fig. 2. Same specimen as in Fig. 1. Direct print using a Durst 1000 enlarger. x 2.5.

from the date of collection to the date of storage as a permanent mount.

O'Brien (1974) has pointed out that some time may be saved by autoclaving the material in hydroxide. Subsequent to this we have found that the drying time of nearly three weeks for mounting media such as Canada Balsam, Euparal, Permout and Xam can be cut to less than one day by using polyester resin. An added advantage of this procedure is that the monomer of the resin is itself an effective clearing agent. This not only shortens the time needed in clearing, but also produces a specimen with exceptional clarity and reproducibility for photographic work (Figs 1, 2).

Methods

While the basic technique described below was originally outlined by Foster (1952) and incorporates the modifications of others (Chan-

drasekharam 1972,¹ Hickey 1973), the procedure is presented in its entirety here to facilitate its usage. The method is equally applicable to fresh or dried leaves, with perhaps a slight advantage to the dried material, due to chlorophyll breakdown. All times given are approximate, and will vary with the nature of the material being cleared.

1. Soak leaves in 15% potassium or sodium hydroxide solution until they are decolorised, changing the solution every two days or as necessary. The most satisfactory vessels for this are glass petri dishes, with the leaves placed in them under discs of plastic mesh screening to prevent flotation. The time for decolorisation varies with the specimen from four days to four weeks. Strongly resinous or tanniferous leaves will usually take longest.

2. Wash the leaves under a gentle stream of water and transfer to saturated chloral hydrate until totally clear. This should take from two

to seven days, with slight warming hastening the procedure on slow material.

3. Wash leaves again (as in step two) and transfer to a dehydration series consisting of 10%, 50% and 90% aqueous ethanol. Finally transfer to absolute alcohol. This series should take less than one day.

4. Stain in 1% Safranin in 1:2 absolute alcohol/toluol solution. Stain for three to five minutes or until all vascular tissue has taken up colour.

5. Destain the mesophyll in alcohol/toluol taking care not to destain the ultimate venation. This step determines the final contrast between the mesophyll and the vascular tissue and is consequently critical. Experience has shown that mounted leaves having an absolute absorbance of 1.2 to 2.5 at 525 nm yield the best density for transmitted light photography. Absorbances were measured on a Beckman Acta CIII Spectrophotometer with the leaves at the back of the sample chamber. By comparison, leaves having an absorbance of less than 1.0 proved too light for acceptable reproduction, while those with an absorbance of more than 2.5 proved too dense. As a comparison, the absorbance of 0.2% safranin measured over a 1.0 cm light path is 1.9, and a one cm cuvette of this solution may be used as a control while destaining.

6. Transfer correctly destained leaves to acetone for about ten minutes to remove remaining alcohol/toluol.

7. Without allowing the leaf surface to dry, transfer the leaf to uncatalysed resin monomer¹. The monomer acts as a final clearing agent and normally renders leaves quite transparent in 30 minutes. Should the leaf surface dry during transfer to the monomer, the resulting opacity may be cleared by leaving the leaf overnight in the monomer. This monomer bath is reusable, and consequently this step is best carried out away from direct sunlight and under fairly cool conditions to prevent polymerisation of the resin.

8. Prepare the final mounting medium by adding about 5% of MEKP catalyst to fresh resin monomer. This is best accomplished by mixing in a small glass phial and rolling between the hands to combine the two components. Such gentle mixing prevents the formation of bubbles in the mountant.

9. Drain the leaf of excess monomer and mount between two glass slides. Setting should take about 2 hours at 30°C. Higher temperatures give shorter setting times but increase the risk of the resin parting from the glass.

10. When the mount is dried, excess resin may be removed with a sharp razor blade or scalpel. Small particles or thin films may be removed with xylene or acetone.

Discussion

Having obtained a permanent mount of a leaf with maximum transparency, it is then necessary to reproduce the venation pattern with as great a degree of contrast as possible for comparison with fossil material. For normal photographs, a Leitz "Aristophot" 4 by 5 sheet film camera with a Macro-Dia attachment for transmitted light gave excellent results (Fig. 1). With a large format camera such as this it is possible to photograph the leaf at nearly life size. The negative can then be contact printed and maximum detail is obtained.

Since maximum contrast between the veins and the mesophyll tissue is desirable, however, the subtle shadings of greys provided by this method proved unnecessary. Galavazi (1965) made brief reference to the direct use of an enlarger for plant material cleared in methyl benzoate. Dilcher (1974) also successfully used this technique on skeletonized and hydroxide cleared leaves. This technique was also admirably suited for our cleared leaves. The mounted leaves fit easily into the negative carrier of a Durst 1000 enlarger and the image can be directly printed on photographic paper. This technique produces a dark-light reversed image (Fig. 2), but as the pattern is the important aspect, this reversal is immaterial.

To achieve maximum contrast, a number of different stains were tried (Morley 1949). Bismarck Brown gave perhaps the greatest contrast, but stained very unevenly. Safranin gave very nearly equal contrast, and had the advantage of staining much more uniformly. Grade four photographic paper was used to give the best contrast in printing.

While the above methods approximately halve the time of the total clearing and mounting procedure, it can still take up to three

¹ For mounting the specimens, Mulfoid EX-80 polyester resin was used. It is available from Mulfoid Plastics Pty Ltd., 25 Anzac Highway, Keswick, S. Aust. 5035.

weeks for difficult leaves. Work is in progress using a lacto-phenol clearing method and it is believed that a procedure has now been found to permanently mount specimens cleared in

this fashion. Even with this success, however, the hydroxide method, though longer, still appears to give better results with a wider spectrum of leaf types.

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PORPHYRA AND PORPHYROPSIS (RHODOPHYTA) IN SOUTHERN AUSTRALIA

BY H. B. S. WOMERSLEY AND ELSIE CONWAY†*

Summary

WOMERSLEY, H. B. S., & CONWAY, Elsie (1975) .-*Porphyra* and *Porphyropsis* (Rhodophyta) in southern Australia. *Trans. R. Soc. S. Aust.* 99(2), 59-70, 31 May, 1975.

Two epilithic species of *Porphyra*, *P. columbina* and *P. lucasii*, occur on southern Australian coasts, mainly during winter; their seasonal morphology and distribution are described. One epiphytic species, the little-known *P. woolhousiae*, is described from additional collections, some of which are reproductive. *Porphyropsis minuta* sp. nov., epiphytic on *Pterocladia capillacea* and other cartilaginous red algae, is also described.

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Introduction

Porphyra is common during winter on the south-eastern coast of Australia, and a brief account of *P. columbina* Montagne and *P. lucasii* Levring was given by Levring (1953). Both these species occur on rock or firm substrates and are monostromatic with a single rhodoplast per cell. Levring also described *P. denticulata* Levring from Queensland, recorded *P. naiadum* Anderson (now *Smithora naiadum* (Anderson) Hollenberg) from New South Wales, and repeated the original record of *P. woolhousiae* Harvey from Tasmania.

Since it is largely a winter form, *Porphyra* has often been omitted from ecological accounts. *P. umbilicalis* (= *P. columbina*, from Cribb 62.5 in ADU) was, however, recorded by Cribb (1954, p. 30) as forming an almost pure association during winter and spring, on fairly rough-water coast at Port Arthur, Tasmania, and *P. columbina* was recorded by Guiler (1954, p. 64) from Blackman's Bay (near Hobart), Tasmania. Womersley & Edmonds (1958, p. 247) recorded *P. columbina* and *P. umbilicalis* (= *P. lucasii*) as winter forms, mainly on the south-eastern coast of South Australia, but sporadically further west.

This paper deals only with southern Australian species of *Porphyra* and the related genus *Porphyropsis*. It is hoped that this presentation of the species will stimulate cultural studies to elucidate further their relationships.

Genus PORPHYRA C. Agardh

Key to Southern Australian Species

1. Blades delicate, rose-pink, ovate to lanceolate, epiphytic on certain brown (or red) algae in the upper sublittoral

P. woolhousiae Harvey

1. Blades lanceolate or ribbon-like, becoming umbilicate, grey- to red- or dark-purple, growing on rock or hard substrates 2
2. Thallus fairly tough, retaining its form when old, shrinking on drying and not adhering strongly to paper; usually over 45 μ m thick; carposporangial† groups prominent, scattered, with vegetative cells among the groups; spermatangia occurring irregularly around the margin

P. columbina Montagne

2. Thallus usually delicate, disintegrating when old, adhering closely to paper and not markedly shrinking on drying; usually 20–30 μ m thick; carposporangial groups usually not prominent; spermatangia occurring in (usually) narrow, elongate strips, extending inwards from the apical and side margins of the thallus

P. lucasii Levring

***Porphyra woolhousiae* Harvey 1863, pl. 265.**

J. Agardh 1883: 59. De Toni 1897: 15; 1924: 12. Guiler 1952: 84. Lucas 1909: 20; 1929: 15.

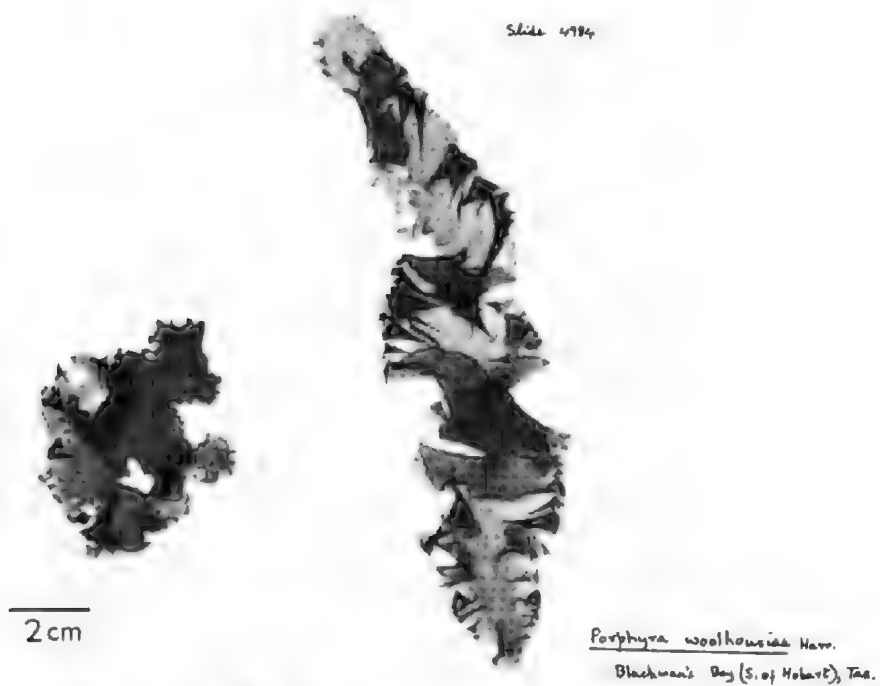
FIGS 1, 2

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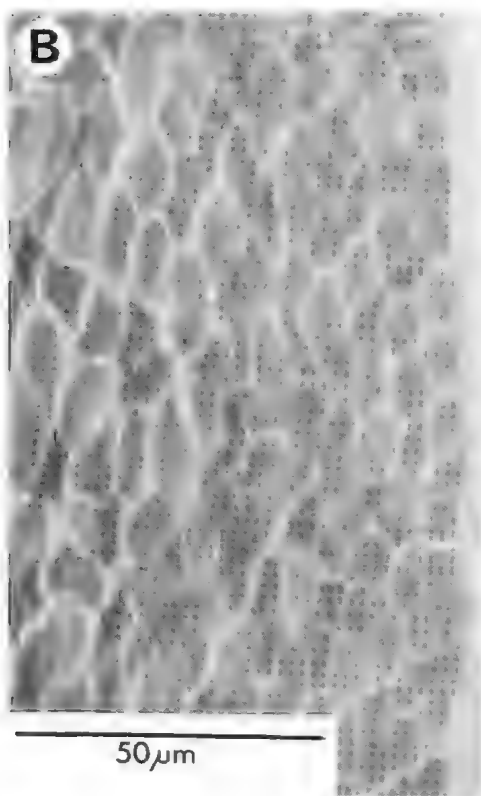
† Department of Botany, University of British Columbia, Vancouver, Canada.

‡ Although the true nature of the reproductive bodies in *Porphyra* is not fully understood, the classical terms carposporangia and spermatangia are used here to avoid confusion (Conway 1964).

A



B



C

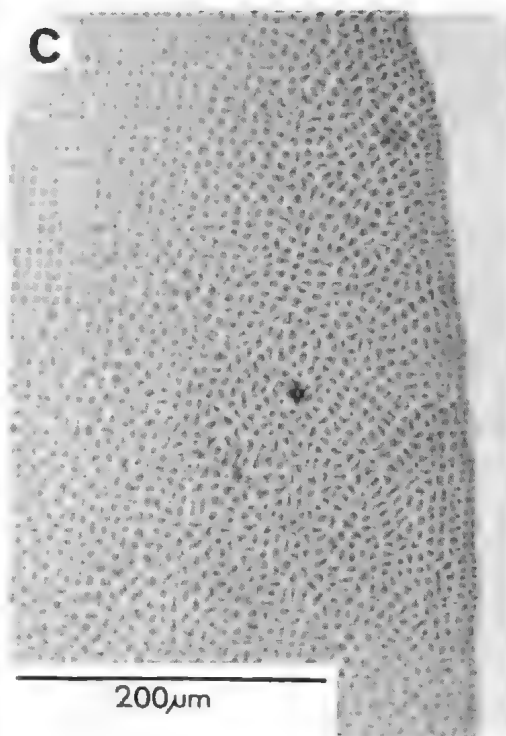


Fig. 1. *Porphyra woolhousiae*. A. Blackman's Bay, Tas. (ADU, A44234). B. Thallus margin, from the type. C. Thallus with margin (A44234).

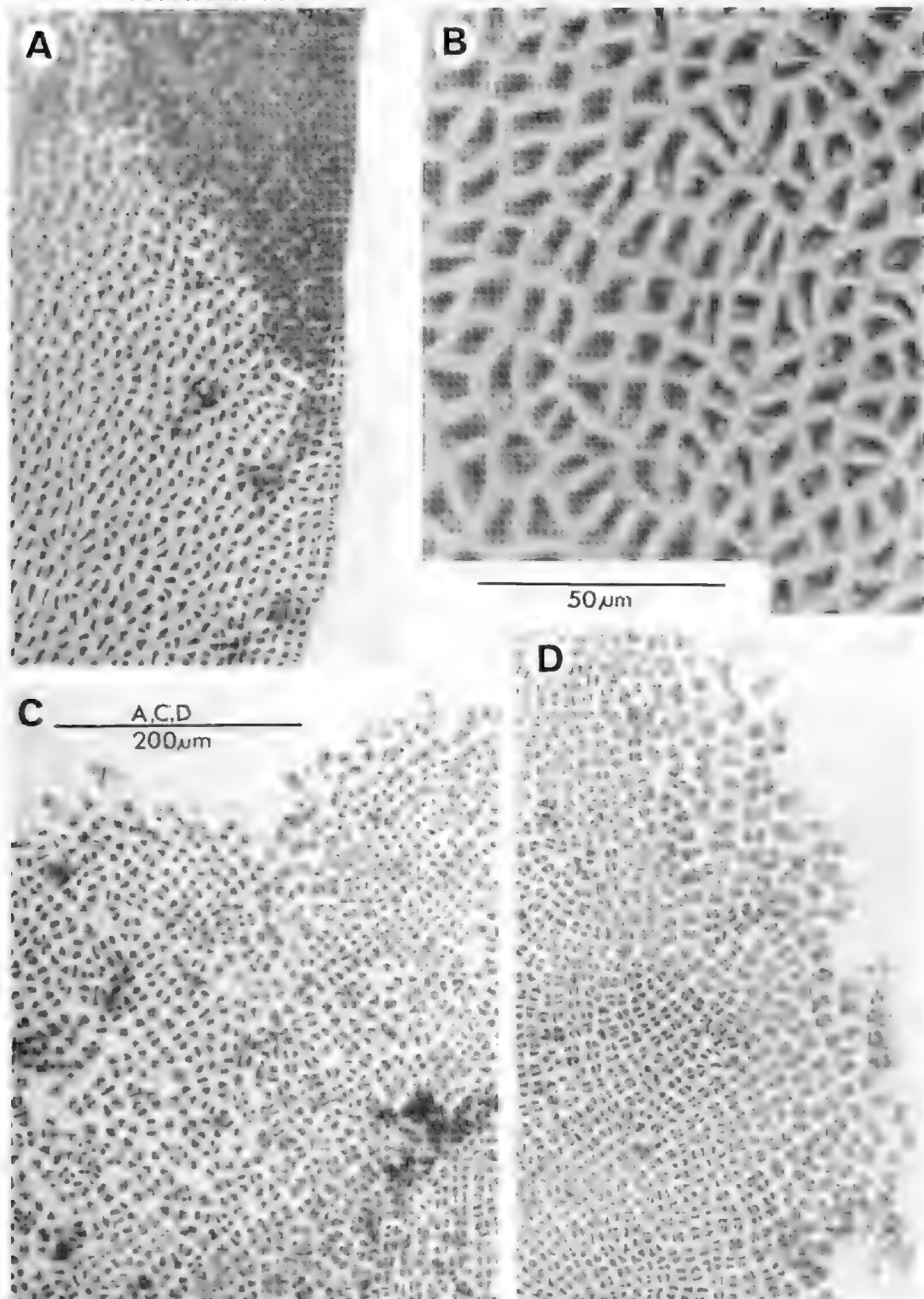


Fig. 2. *Porphyra woolhousiae*. A. Thallus with area of darkly-staining reproductive cells. (Blackman's Bay, Tas., ADU, A44234). B. Cell arrangement in older part (A44234). C. Thallus margin with liberation of reproductive bodies (St Kilda, S. Aust., ADU, A42722). D. Margin with spermatangia (A42722).

Thallus (Fig. 1A) epiphytic on brown algae or rarely on red algae, to 17 cm high and 4 cm broad, front irregularly ovate or cuneate-elongate when young, to broadly expanded or elongate with curved margins which are gently convolute in older plants (e.g. the type), delicate, with one to a few blades arising from a rhizoidal holdfast, rose-red to rose-purplish.

Monostromatic, (12–) 16–24 μm thick, cells isodiametric to slightly elongate in sectional view, each with a single, laminate or stellate rhodoplast, with a pyrenoid. Growth by a marginal meristem (Figs 1B,C, 2A) and by intercalary divisions: margins meristematic, with anticlinal rows of cells; older parts with cells often in rows but becoming irregular, with cells often polygonal or angular (Figs 1B, 2B), some rounded to ovoid, often with adjacent cells unequal in size. Marginal cells isodiametric to slightly elongate, angular, 6–10 μm across; cells in older parts isodiametric to twice as long as broad, 10–16 (–20) μm across.

Reproductive bodies (Fig. 2A,C) formed in marginal areas, apparently singly, spherical to slightly ovoid, 12–17 μm across, usually with a stellate rhodoplast.

Spermatangia (Fig. 2D) forming well defined, irregular, patches near the thallus margins, the whole patch when mature tending to deliquesce with numerous spermatangia irregularly arranged; spermatangia originally formed in packets of (16–) 32–64, in two tiers, individually 2–4 μm across.

Type locality: Tasmania.

Type: Herb. Harvey, TCD (presented by Miss Woolhouse of Sheffield).

Distribution: As well as the type, this species is known from St Kilda, S. Aust., on *Gigartina*(?) on *Posidonia*, 1½ m below low tide level (S. Lewis, 23.viii.1972; ADU, A42722); Mallacoota, Vic., on *Scytothamnus australis* (Ducker and King, 15.ii.1970; MELU, 20652); Deal I., Bass Strait, on *Perithalia caudata* (King, 23.xi.1969; MELU, 21357); Curtis I., Bass Strait, on *P. caudata* (King, 8.ii.1971; MELU, 21358); and from Blackman's Bay (S. of Hobart), Tas., drift (Tyler, Oct.(?) 1973; ADU, A44234).

The type of *P. woolhousiae* is a well-developed specimen to 15 cm high, as in the Blackman's Bay, Tas., specimen, whereas St Kilda specimens are 2–4 cm high, the Mallacoota specimens are only 1–2 cm high and those from Bass Strait less than 1 cm high;

the latter appear to be juvenile. All these, including the type, show similar cell structure and presence of marginal growth on young parts and often also on mature thalli. This marginal meristem is not apparent on the other southern Australian species or on most other species placed in *Porphyra*. A fragment of the type studied is not fertile, but the other specimens show characteristic spermatangial groups which tend to deliquesce, and from marginal areas the contents of each cell appear to be liberated as a reproductive body. *P. woolhousiae* has a typical *Porphyra* base with one or a few fronds attached by rhizoids from the basal thallus cells, and in most features agrees well with *Porphyra*. If, however, it is confirmed that the carposporangia are formed singly, then relationships with the genus *Porphyrella* Smith & Hollenberg (1943, p. 215) must be considered, though Conway & Wylie (1972) have shown that the New Zealand *Porphyra subumens* does not form packets of carposporangia.

While it is desirable that mature plants on *Macrocystis*, corresponding to the type, be studied in detail, and their reproduction followed in culture, the other records are sufficiently similar to be placed under *P. woolhousiae* with some confidence. Most are epiphytic on brown algae, either on marginal spines or on spinous branchlets, and this habit may be characteristic for the species.

P. woolhousiae has been recorded from New Zealand (Levring 1955, p. 412), followed by D. J. Chapman (1962, p. 129), V. J. Chapman (1969, p. 20) and Adams (1972, p. 67). However Adams, following notes of E. Conway in CHR, expresses doubt as to whether the New Zealand records are not *P. columbina* in an abnormal habitat.

The New Zealand specimens growing on *Macrocystis* (and possibly *Ecklonia* and *Scytothamnus*) need further comparison with the Australian plants referred to *P. woolhousiae*. Ones from Hokio Beach, Levin, N.Z., on *Macrocystis* (Moore, 17.xi.1946; CHR, 55566), determined by Levring (1955, p. 412) as *P. woolhousiae* (accompanied by notes of E. Conway (1971) that they might be young plants of *P. columbina*), agree fairly well with *P. woolhousiae* as now known from the Australian plants. They are similar in form, in thickness and cell arrangement, and in having a meristematic margin, but their reproduction is inadequately known.

Further comparisons between Australian and New Zealand specimens epiphytic on *Macrocystis* are clearly needed.

Skottsberg (1923, p. 4) recorded *P. woolhousiae* from the Falkland Islands, also on spines of *Macrocystis*, and his account shows similarities with the above description; details are not adequate for a full comparison. Hamel (1928, p. 55) recorded it from Kerguelen I., and Pujals (1963, p. 8) gives records from South America.

Porphyra columbina Montagne 1842: 14; 1845: 33, pl. 9, fig. 2. J. Agardh 1883: 70, pl. II, figs 65–66. V. J. Chapman: 1969: 22. Dawson, Acleto and Foldvic 1964: 32, pl. 61B. Guiler 1952: 84. Hamel 1928: 51. Kuetzing 1849: 693; 1869: 29, pl. 80e,f. Laing 1928: 39, figs 1–7. Levring 1953: 464, figs 2–4; 1955: 410; 1960: 29. Pujals 1963: 8.

Wildemanian columbina (Mont.) De Toni 1897: 22.

P. umbilicalis sensu Cribb 1954: 30.

FIGS 3, 4

Thallus fairly tough, varying from ribbon-like (Fig. 3A), often with undulate margins, to broader forms, sometimes furcate, and usually umbilicate (by loss of upper parts and basal proliferation) (Fig. 3B) on rough-water coasts. Thallus often markedly shrinking on drying and usually not adhering closely to paper. Variable in size and width, reaching 40 cm long and 30 cm across. Colour varying from grey-red to red-purple.

Monostromatic, 35–50 μm thick, cells isodiametric in section and with a single axile, pyrenoid-bearing, rhodoplast. Cells 10–15 μm across in surface view (Fig. 4A), isodiametric to slightly elongate, more or less in rows but becoming irregularly arranged, separated by a gelatinous matrix $\frac{1}{2}$ –1 times as wide as cells.

Carpusporangial groups prominent (Fig. 4C), of varying shades of red, forming irregular marginal areas with vegetative cells intermingled, (8–) 32–64 carpusporangia per group, often giving an irregularly granular ("spotty") red appearance to reproductive areas.

Spermatangial groups (Fig. 4B, C) scattered among the carpusporangial groups and in older plants occupying the marginal part of the thallus; not occurring in elongate strips as in *P. lucasii*.

Type locality: Auckland I. (D'Urville).

Type: PC (Herb. Montagne).

Distribution: From Elliston, S. Aust. to Sydney, N.S.W. and around Tasmania; New Zealand, Auckland Islands and other sub-antarctic islands.

P. denticulata Levring from southern Queensland is probably not distinct from *P. columbina* and represents the range extreme of *P. columbina*.

P. columbina is the commonest intertidal species of *Porphyra* in New Zealand and in eastern southern Australia, where it occurs at a lower to mid (sometimes upper) eulittoral level on rough-water coasts. In Australia it is essentially a winter form, persisting as late as December (rarely to February in Bass Strait) in cooler summers and reappearing in about May.

Porphyra lucasii Levring 1953: 469, figs 6H–L, 7.

P. umbilicalis sensu Guiler 1952: 84. Womersley 1950: 162.

FIGS 5, 6

Thallus usually fairly delicate, varying from lanceolate or ribbon-like (Fig. 5A) to broadly ovate or cordate (Fig. 5B), simple or irregularly lacinate or basally branched, sometimes becoming umbilicate from basal proliferation, usually adhering to paper and not shrinking on drying; to 10 cm long and 15 cm broad, margin smooth to undulate.

Monostromatic, 20–30 μm thick, cells with a single axile, pyrenoid-bearing, rhodoplast. Cells 8–15 μm across in surface view (Fig. 6A), mostly irregularly arranged, separated by gelatinous matrix $\frac{1}{2}$ –1 times as wide as cells.

Carpusporangial groups (Fig. 6C) usually not prominent, covering areas around the spermatangial strips toward the margin of the thallus, without conspicuous intermingled vegetative cells, about 8 carpusporangia per group. Carpusporangial groups often apparently developing later than spermatangial strips, thus giving an impression of dioecism.

Spermatangial groups (Fig. 6B, C) occurring as well-marked elongate strips (Fig. 5B) extending in from the apical regions and side margins of the thallus; strips from a few mm to 2 cm long, 1–5 mm broad. Margin becoming "fringed" following shedding of spermatangial strips.

Type locality: Bunbury, W. Aust.

Type: Herb. Levring, Goteburg. (Isotype in ADU, A42700).

Pl. 2, col. 1

A

Porphyra
Little Dip (S. of Robe), S. Aust.
M.A. culminal
15.5.1972
Coll. H.B.S. & Elsie Conway

B

Porphyra columbina Mont.
Cape Lannes, S. Aust.
M.A. culminal
7.5.1972

Coll. H.B.S. & Elsie Conway

Fig. 3. *Porphyra columbina*. A. Ribbon-like forms, early winter. Little Dip, Robe, S. Aust. (Womersley, 15.v.1972; ADU, A42203). B. More umbilicate forms from spring. Cape Lannes, S. Aust. (Womersley, 7.x.1972; ADU, A42768).

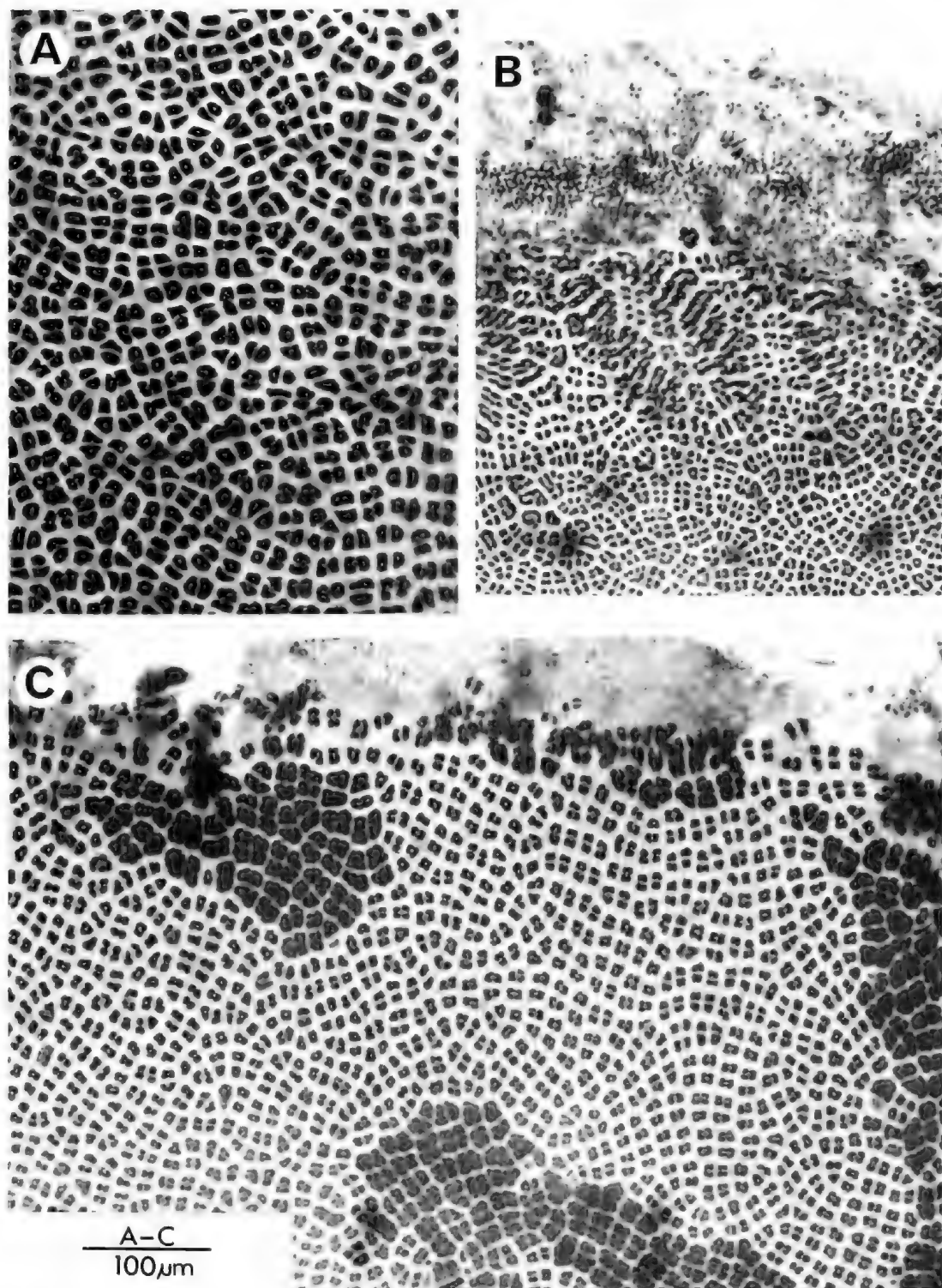


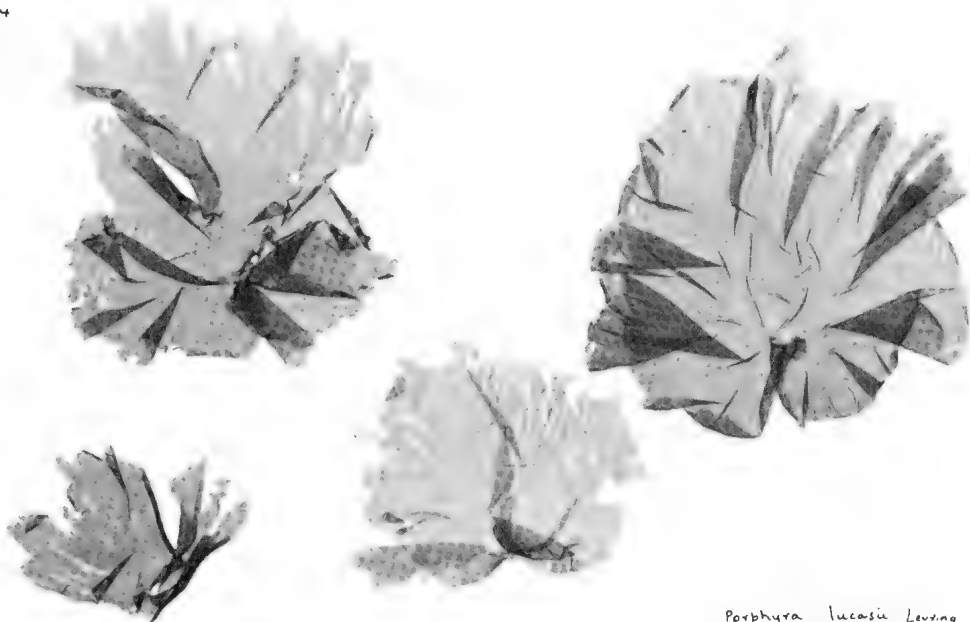
Fig. 4. *Porphyra columbina*. A. Vegetative cells. Nora Creina, S. Aust. (Womersley, 3.ix.1971; ADU, A39559). B. Spermatangial marginal area (A39559). C. Area with carposporangial groups and young spermatangia (A39559).

A42,637
A



Porphyra lucasii Leving
Port Stanvac, S Aust
Mid sublittoral on piles
1 IX 1972
Coll A Lewis
Det. H.B.S. Womersley

A42,764
B



Porphyra lucasii Leving
Robe, S. Aust.
Mid sublittoral, in bay near
8.8. 1972

Coll & Det. H.B.S. Womersley

Fig. 5. *Porphyra lucasii*. A. Ribbon-like forms. Port Stanvac, S. Aust. (Lewis, 1.ix.1972; ADU, A42637). B. Broadly ovate forms showing spermatangial strips. Robe, S. Aust., in bay (Womersley, 8.x.1972; ADU, A42764).

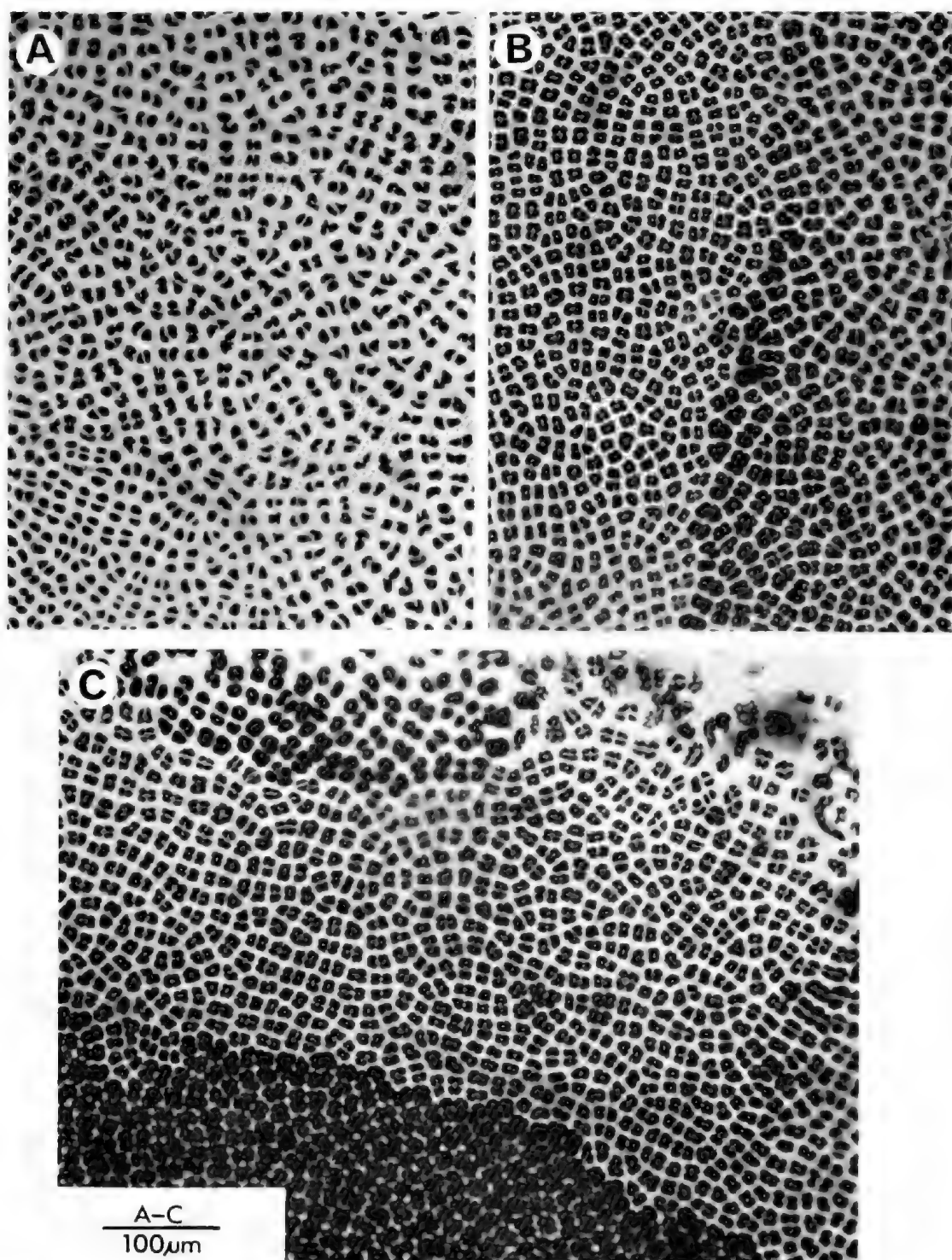


Fig. 6. *Porphyra lucasii*. A. Vegetative cells (ADU, A42764). B. Edge of a spermatangial strip with vegetative and carposporangial cells on the right (A42764). C. Part of a spermatangial strip releasing spermatia above and with carposporangial groups below (A42764).

Distribution: From Cottesloe, W. Aust. to Western Port Bay, Vic. and the north and east coasts of Tasmania.

P. lucasii is the common *Porphyra* of calm to moderately rough waters, being replaced by *P. columbina* where surf action is strong. It is essentially a winter plant of the mid to upper eulittoral, with old plants being found in October, *P. lucasii* is found within calmer bays such as Port Phillip Bay and Western Port, Vic., whereas *P. columbina* occurs on rough-water coasts.

Genus PORPHYROPSIS Rosenvinge

Porphyropsis minuta sp. nov.

Thallus epiphytic on certain Rhodophyta with a firm surface, developing from a subparenchymatous holdfast to form a hollow, sub-spherical to ovoid bladder (Fig. 7A), later opening above to form irregular, monostromatic membranes often with convolute margins. Color greenish-brown to purplish, not rose-red.

Bladders up to 1 (–2) mm across, torn membranes to 5 (–8) mm high and across. Cell divisions intercalary. Holdfast 50–100 (–200) μm across, formed of irregularly arranged cells without rhizoidal extensions. Cells of bladder (Fig. 7B, C) often paired or in fours following division, and lying in rows more or less at right angles, sometimes becoming irregularly arranged; membrane about 10 μm thick, cells 3–5 μm across and rounded to somewhat elongate in surface view, slightly ovate in sectional view. Rhodoplast apparently filling the cell, without a pyrenoid.

Monosporangia (Fig. 7B) formed from the whole contents of cells near the margin of the membranes, subspherical to ovoid, 5–7 μm across.

Thallus in Rhodophytis epiphyticus, solido superficie, ex subparenchymato base ortus, primum vesicam cavam, subglobosam vel ovoideam formans deinde superne membranas irregulares monostromaticasque saepe margine convolutis producens. Color brunneo-viridis vel purpureus, sed nunquam carneus.

Vesicae ad 1 (–2) mm latae, membranae laceratae ad 5 (–8) mm altae et latae. Divisura cellularum intercalaris. Basis ad 50–100 (–200) μm lata, ex cellulis sine projecturis rhizoideorum irregulariter compositis formata est. Cellulae vesicae saepe binae vel quaternae post divisionem, seriatim plus minusve rectangularae, interdum irregulariter compositae; membrana circa 10 μm crassa, cellulis ad 3–5

μm latis et aspectu frontali globosis vel aliquantum elongatis, in sectione transversali parum ovoideis. Rhodoplastus ut videtur, cellulam complet, pyrenoide absent.

Monosporangia subglobosa vel ovoidea, 5–7 μm lata, in cellulis prope marginem membranarum formata.

FIG. 7

Type locality: Pearson I., S. Aust., on *Pterocladia capillacea*, upper sub-littoral (Specht, 17.ii.1960).

Type: ADU, A24525.

Distribution: From Garden I., W. Aust. around southern Australia to Bateman's Bay, N.S.W., epiphytic on *Pterocladia capillacea* in upper sublittoral (and pools) on rough-water coasts, and occasionally on *Plocamium angustum*, *P. mertensii* and *Delisea pulchra* in similar habitats.

P. minuta agrees well with *P. coccinea* in the holdfast, form and development of the bladder, and in reproducing apparently only by monosporangia. The cells of *P. minuta* are similar in size to those in *P. coccinea* but are arranged in distinct rows more or less at right angles, in contrast to both *P. coccinea* from Europe (Rosenvinge 1909, p. 69, fig. 9) and *P. coccinea* var. *dawsonii* Hollenberg & Abbott (1968, p. 1239, fig. 5a–c) from California, where the cells are more irregularly arranged but are grouped into elongate, somewhat lenticular patches. The life-history and relationships of the latter taxon have been discussed by Murray, Dixon & Scott (1972), and it is desirable that the Australian plant should be studied in culture.

A further difference is that in *P. minuta* the whole contents of cells near the margins are liberated as monospores, whereas in *P. coccinea* the monospores are cut off from the parent cell by a curved wall, a residual cell remaining when the monospore is liberated. Also, in *P. coccinea* some holdfast cells form rhizoidal extensions whereas this has not been observed in *P. minuta*. The colour of *P. minuta* is always a greenish-brown-purple, never rose-red as in *P. coccinea*.

The only other southern hemisphere record of *Porphyropsis* is by Adams (1972, p. 68) who reported *P. coccinea* var. *dawsonii* from New Zealand. This taxon (e.g. CHR 248053 from Kaikoura, N.Z.; Parsons, 13.xi.1973) has numerous ligulate fronds from a clumped base, each with descending rhizoids. It is not a *Porphyropsis*, but more closely related to *Porphyra woolhousiae*.

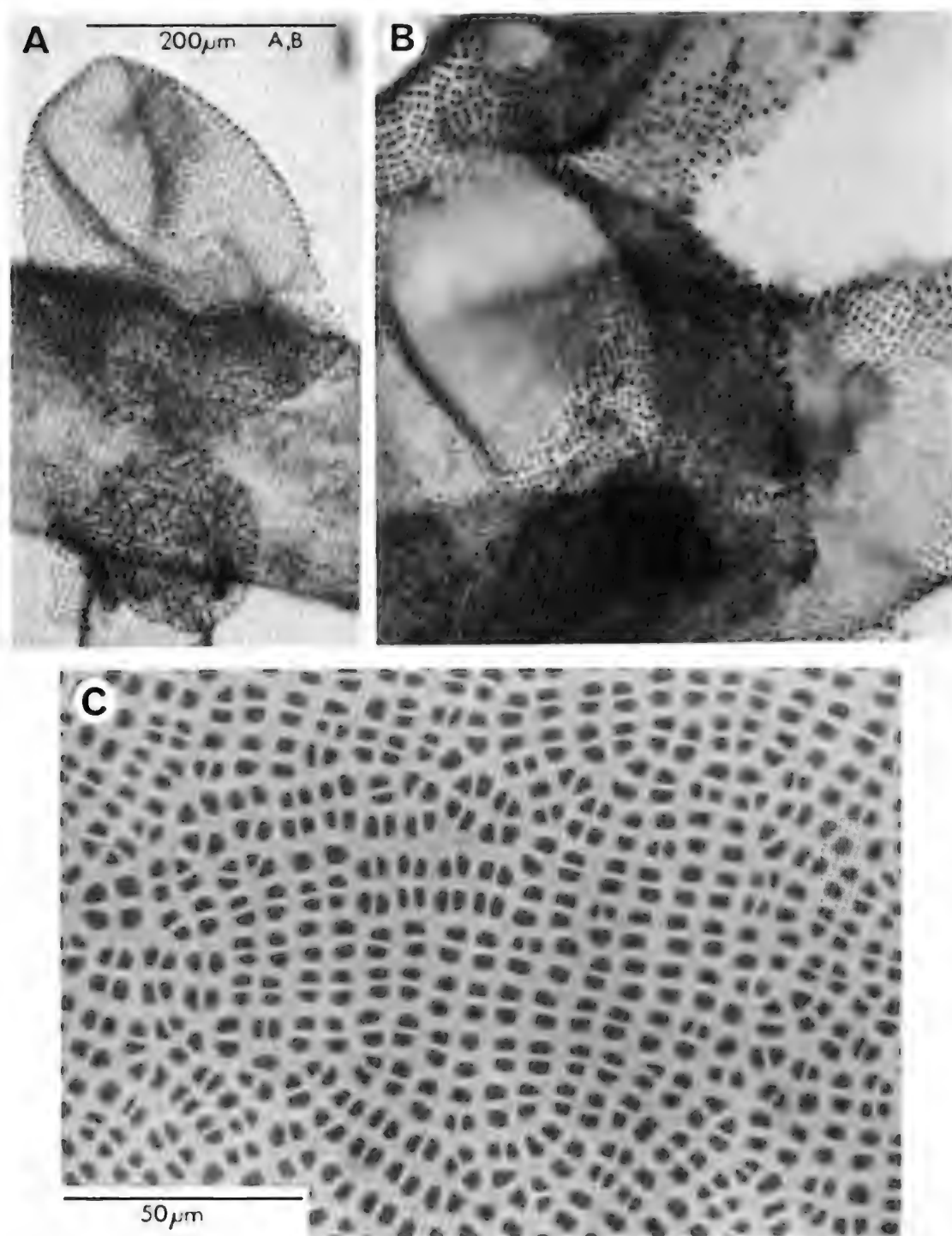


Fig. 7. *Porphyropsis minuta*. A. Small plants, on *Pterocladia*. B. Older membrane, with some cells releasing monosporangia. C. Cell arrangement. (All from the type, ADU, A42525.)

Acknowledgments

We are grateful to Mrs S. C. Ducker (University of Melbourne) who made available collections for study, and to Dr P. Tyler (Uni-

versity of Tasmania) who recollected *P. woolhousiae*. The first author acknowledges provision of technical assistance by the Australian Research Grants Committee.

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THE VERTEBRAE OF FOUR AUSTRALIAN ELAPID SNAKES (SQUAMATA: ELAPIDAE)

BY MEREDITH J. SMITH*

Summary

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In vertebral morphology, the elapid species *Pseudechis porphyriacus*, *Austrelaps superba*, *Notechis scutatus* and *Pseudonaja nuchalis* conform with general descriptions and closely resemble each other. Features not previously noted are that epizygapophysial spines appear on the first 8 to 10 vertebrae, and that bilaterally on every precloacal vertebra a foramen opens through the accessory process near the anterolateral edge of the prezygapophysial facet. No morphometric feature was found to completely separate any two genera, i.e. there was some overlap in the values of all the characters (ratios) studied. However, in general *P. porphyriacus* vertebrae are distinguished by their relatively long accessory processes, *A. superba* by their short accessory processes and lesser width across postzygapophyses, and *N. scutatus* by their greater width across postzygapophyses and shorter neural spines. *P. nuchalis* vertebrae have strong subcentral ridges

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Fossil vertebrae from a Pleistocene deposit differ from *P. porphyriacus*, *A. superba* and *N. scutatus* but resemble *Pseudonaja* in most features. The fossils differ from modern *P. nuchalis* chiefly in having a thicker zygosphen and relatively wider postzygapophyses. As these are features which develop with increasing size of vertebrae, the fossil vertebrae are assigned to the genus *Pseudonaja*.

Introduction

Although snake vertebrae have been recorded from Australian Pleistocene deposits (Lydekker 1888, Merrilees 1968), the only species that has been identified is the Carpet Snake, *Morelia spilotes variegata* Gray (= *Python variegatus*) from Marmor Quarry, Queensland (Longman 1925). No detailed studies have been published of Australian snake vertebrae and the diagnostic characters have not been established. The need to determine the reptile fauna in a Pleistocene cave deposit stimulated the present study.

The sixty-odd Australian species of elapids have been arranged in 29 genera (Worrell 1963) or fewer (McDowell 1967, 1970), but only seven genera contain species with a recorded maximum length of over 0.9 m. As centrum lengths of some of the Pleistocene vertebrae suggested that the specimens from which they were derived must have exceeded 1.5 m, the 22 genera of smaller species (less than 0.9 m maximum length) have not been considered. Nor have *Demansia* (restricted to

the whip snakes by Worrell (1963)), *Hoplocephalus*, and *Oxyuranus* been examined as their range is northern and eastern Australia (Worrell 1963). Specimens have been studied from the remaining four genera, *Austrelaps*, *Notechis*, *Pseudechis* and *Pseudonaja*, which are each represented in southern Australia by one or more common species.

The exact column position of an isolated vertebra is impossible to determine (Johnson 1955) and in elapids, with well-developed hypapophyses on all pre-cloacal vertebrae, division of the pre-cloacal column into regions is virtually impossible. Nevertheless vertebral shape changes along the column, and to identify single vertebrae it is essential to know the range of variation within individuals and species. Auffenberg (1963) based his descriptions and diagnoses on middle pre-caudal vertebrae (determined as such by the relative size of the neural canal) and avoided considering intracolumnar variation. Although Johnson (1955) measured 10 precloacal vertebrae at regular intervals along the column, he assumed

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equal variances (between specimens) of ratios of these measurements and in his comparisons he used only the mean for each specimen. Here, entire vertebral columns have been examined in an attempt to assess the morphological and morphometric variation which occurs within individuals and species, and to find unique specific characters. As most elapids have over 200 vertebrae, the available samples are large and the time required for detailed examination of one individual snake precludes sampling many individuals.

Because taxonomy of species of *Pseudonaja* and *Austrelaps* is confused (Rawlinson 1969, Storr 1964) comparisons are made at the generic rather than species level.

Materials and Methods

A total of 2,123 vertebrae from nine Recent specimens (Table 1) and 556 Pleistocene vertebrae were examined. Of the nine modern specimens, four specimens of *Pseudechis porphyriacus*, one *Pseudonaja nuchalis* (R14064) and one *Notechis scutatus* (R14059) were collected near Armidale, New South Wales; the one *Austrelaps superba* was collected at Uraidla, South Australia. The localities of one *P. nuchalis* (R14065) and one *N. scutatus* (R14058) are unknown.

The common brown snake, *Pseudonaja textilis* (Duméril & Bibron), has been described as a separate species from the western brown snake, *Pseudonaja nuchalis* Günther, but it is not yet clear (Storr 1964) whether they are distinct or are merely races of a single species, *P. textilis*. One clearcut diagnostic feature is the shape of the nasal bones, which are anteriorly concave on the lateral margins in *P. nuchalis* but anteriorly convex in *P. textilis* (Worrell 1963). In R14064 and R14065 the nasals are anteriorly concave and hence are attributable to *P. nuchalis*.

The cleaned skeletons were dried and completely disarticulated for study. The specimens are now lodged in the South Australian Museum, with register numbers as above.

The Pleistocene vertebrae were excavated from an extensive bone deposit in Victoria Cave, Naracoorte, South Australia. The age of this deposit is unknown, but the abundance of extinct marsupials and the absence of remains of aboriginal man suggest that the deposit accumulated during the Pleistocene but was sealed during Recent time. As the vertebrae were collected singly in many locations in the bone deposit, they probably represent

at least several individuals. Visual examination of the fossils revealed that 454 of them were similar to each other in shape, and distinctly different from the rest, which were of several kinds. The latter, heterogeneous group will be discussed in a later paper. Of the larger group of 454, the 80 most complete were examined in detail and measured in the same way as the modern vertebrae.

Because reptiles grow throughout their life, absolute dimensions of the vertebrae are of little use in comparing individuals or species. Ratios between dimensions have been calculated, the denominator being vertebra length in most comparisons. Mean values of ratios have been prepared independently for each individual snake, and are given as mean, \bar{x} , \pm standard error, followed in brackets by the number of vertebrae measured. The non-independence of measurements of different vertebrae of the one individual precludes statistical comparison of these samples (Siegel 1956).

From a preliminary study of numerous characters of snake vertebrae, characters were selected that vary between species within the family Elapidae, exhibit low intracolumnar variation and are well preserved in fossils. To establish variation throughout the column, every fifth vertebra was measured in two specimens of each of *P. porphyriacus*, *P. nuchalis* and *N. scutatus*, and one *A. superba*.

Descriptive techniques and terminology follow Auffenberg (1963). Measurements were made to 0.1 mm with dial calipers, as in Fig. 1:

- pr-po Length between zygapophyses—distance between most anterior point of prezygapophysis to most posterior point of postzygapophysis.
- ap-ap Width across accessory processes—distance between outermost tips of accessory processes.
- po-po Width across postzygapophyses—distance between outermost points of the postzygapophysial facets.
- prl Length of prezygapophysis—the longest diameter of the prezygapophysial facet (even though this was almost perpendicular to the long axis of the centrum).
- pr Width of prezygapophysis—the maximum diameter at right angles to the length of the prezygapophysis (the prezygapophysial width being almost parallel to the long axis of the centrum).

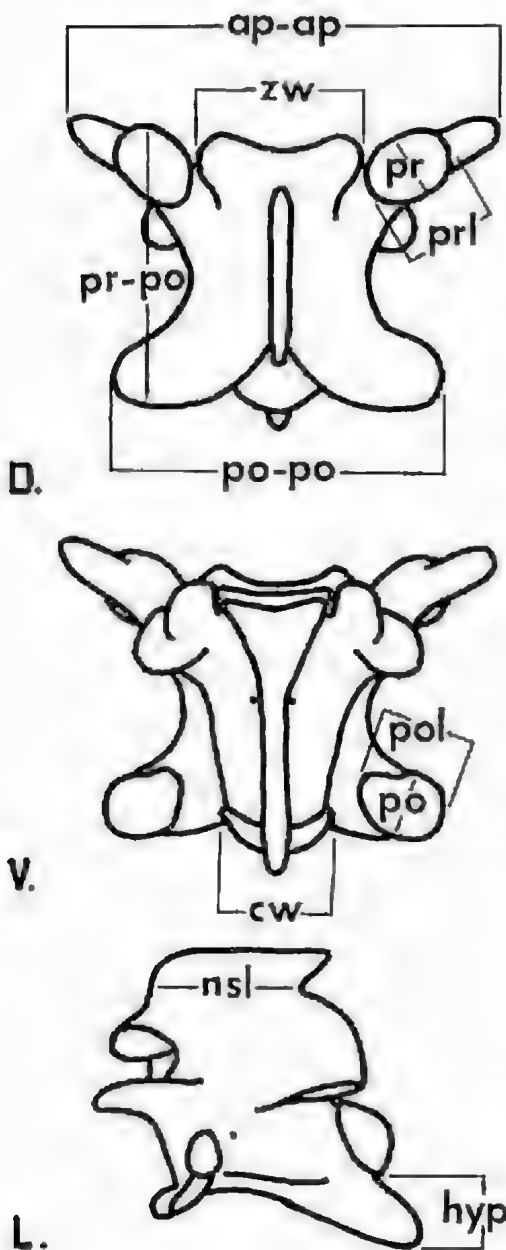


Fig. 1. Dorsal (D), ventral (V) and lateral (L) views of an elapid vertebra showing where measurements were taken.

- pol Length of postzygapophysis—the longest diameter of the postzygapophyseal facet (even though this was almost perpendicular to the long axis of the centrum).
- po Width of postzygapophysis—the maximum diameter at right angles to the length.

- nsl Minimum length of neural spine—this usually occurred about halfway up the spine, as the dorsal edge overhangs posteriorly and/or anteriorly.
- zw Width of zygosphenic—the maximum width of the tenon.
- cw Width of condyle—the maximum diameter in the transverse plane.
- hyp Length of hypapophysis—the vertical distance from the lower edge of the condyle to the tip of the hypapophysis.

Results

The vertebrae conform with the general descriptions of Aussenberg (1963), Hoffstetter & Gasc (1969) and Johnson (1956):

Pseudechis porphyriacus (Shaw)

The number of preloacal vertebrae (Table 1) is consistent with the number of ventral scales (184, according to Worrell 1963).

In every preloacal vertebra, the width across postzygapophyses exceeds the length between zygapophyses (Fig. 2). The hypapophysis arises near the lip of the cotyle, extends as a low lamella for about two-thirds the length of the centrum and then deepens sharply before tapering to a sharp point which does not much exceed the posterior surface of the condyle in any but the most anterior vertebrae. The hypapophyses of the anterior vertebrae are very long; they decrease in length fairly uniformly along the column (Fig. 2). The subcentral ridges are low and rounded. The dorsal articular facet of the paradiapophysis projects as a little round dome; the lower facet is saddleshaped. The prominent parapophyseal processes are rounded anteriorly. They do not extend closer to the midline than the most lateral lip of the cotyle. Interzygapophyseal ridges are faintly distinguishable. The neural spine is a low, laterally-compressed blade, its dorsal edge parallel with the long axis of the vertebra, its anterior edge almost vertical and its posterior edge overhanging.

The minimum length of the neural spine is about half the length between the zygapophyses [\bar{x} $0.53 \pm .0056$ (35); \bar{x} $0.55 \pm .0049$ (36)] (Fig. 3). The neural arch is slightly wider than high. The neural arches of most of the vertebrae do not extend backwards to form epizygapophyseal spines, but such spines are well developed on the first five vertebrae and are distinguishable on the sixth to tenth. The cotyles and condyles are nearly round, but are slightly flattened dorsoventrally. The width of the condyle is about one third of the length

TABLE 1

Total length, snout-to-vent length and number of vertebrae of specimens of four species of elapids

| Species | SAM register number | Sex | Total length (mm) | Snout-vent length (mm) | Number of vertebrae | | | |
|--------------------------------|---------------------|---------|-------------------|------------------------|---------------------|---------|--------------|--------|
| | | | | | Pre-cloacal* | Cloacal | Post-cloacal | Total* |
| <i>Pseudechis porphyriacus</i> | R14060 | no data | 1220 | no data | 181 | 8 | >42 | >231 |
| | R14061 | no data | 1375 | no data | 182 | 6 | 52 | 240 |
| | R14062 | no data | 1120 | no data | 182 | 5 | >30 | >217 |
| | R14063 | no data | 1070 | 890 | 177 | 5 | 48 | 231 |
| <i>Austrelaps superba</i> | R14066 | ♀ | 515 | 433 | 143 | 4 | 42 | 189 |
| <i>Notechis scutatus</i> | R14058 | ♂ | 930 | 775 | 174 | 5 | 58 | 237 |
| | R14059 | no data | no data | 800 | 178 | 5 | 52 | 235 |
| <i>Pseudonaja nuchalis</i> | R14064 | ♂ | 1555 | 1300 | 204 | 6 | 60 | 270 |
| | R14065 | no data | 1100 | 910 | 206 | 5 | 62 | 273 |

* Atlas-axis complex not included in this count.

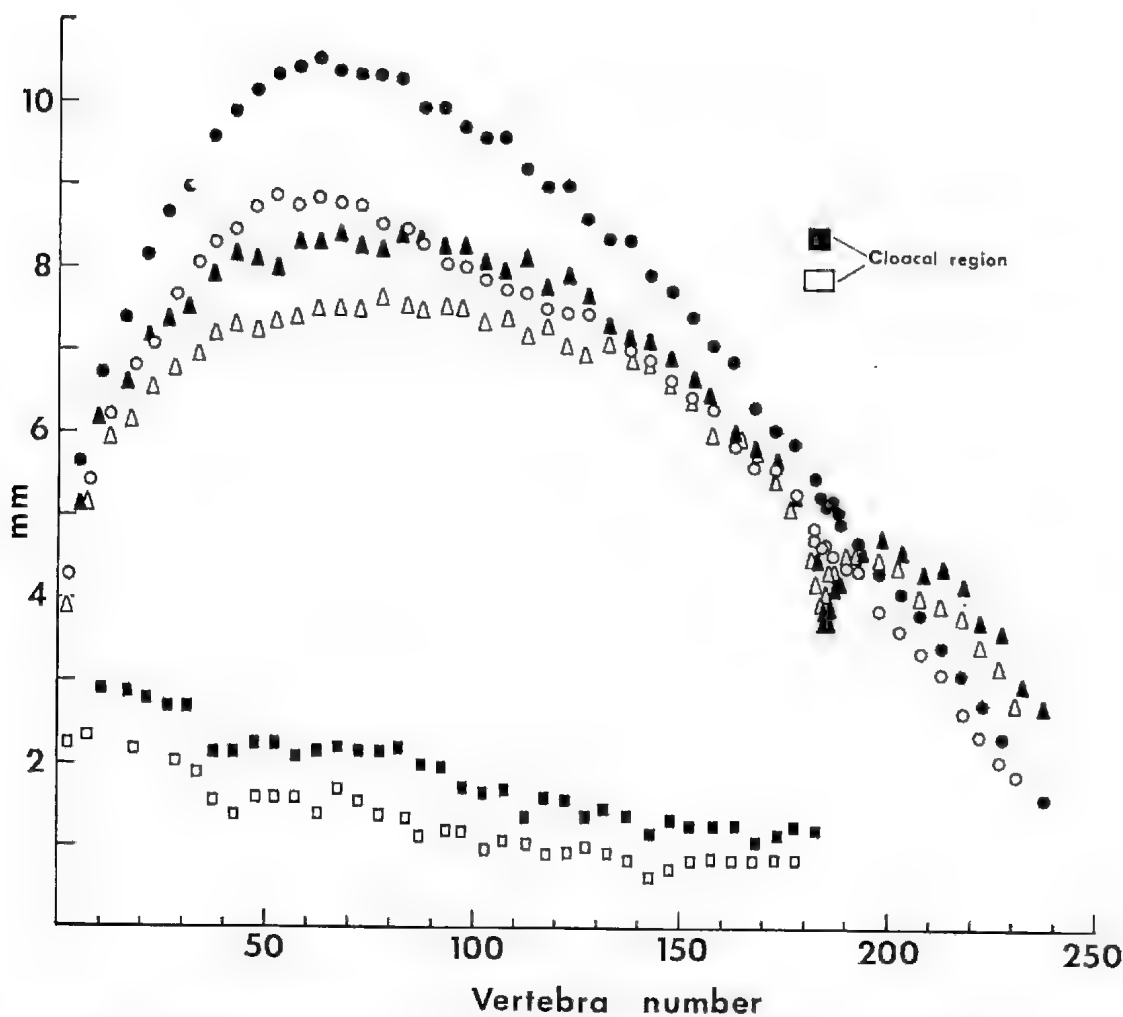


Fig. 2. Variation throughout the vertebral column in (a) length between zygapophyses (\triangle \blacktriangle), (b) width across postzygapophyses (\circ \bullet) and (c) length of hypapophysis (\square \blacksquare) of two specimens of *Pseudechis porphyriacus*. Hollow symbols R14060, solid symbols R14061.

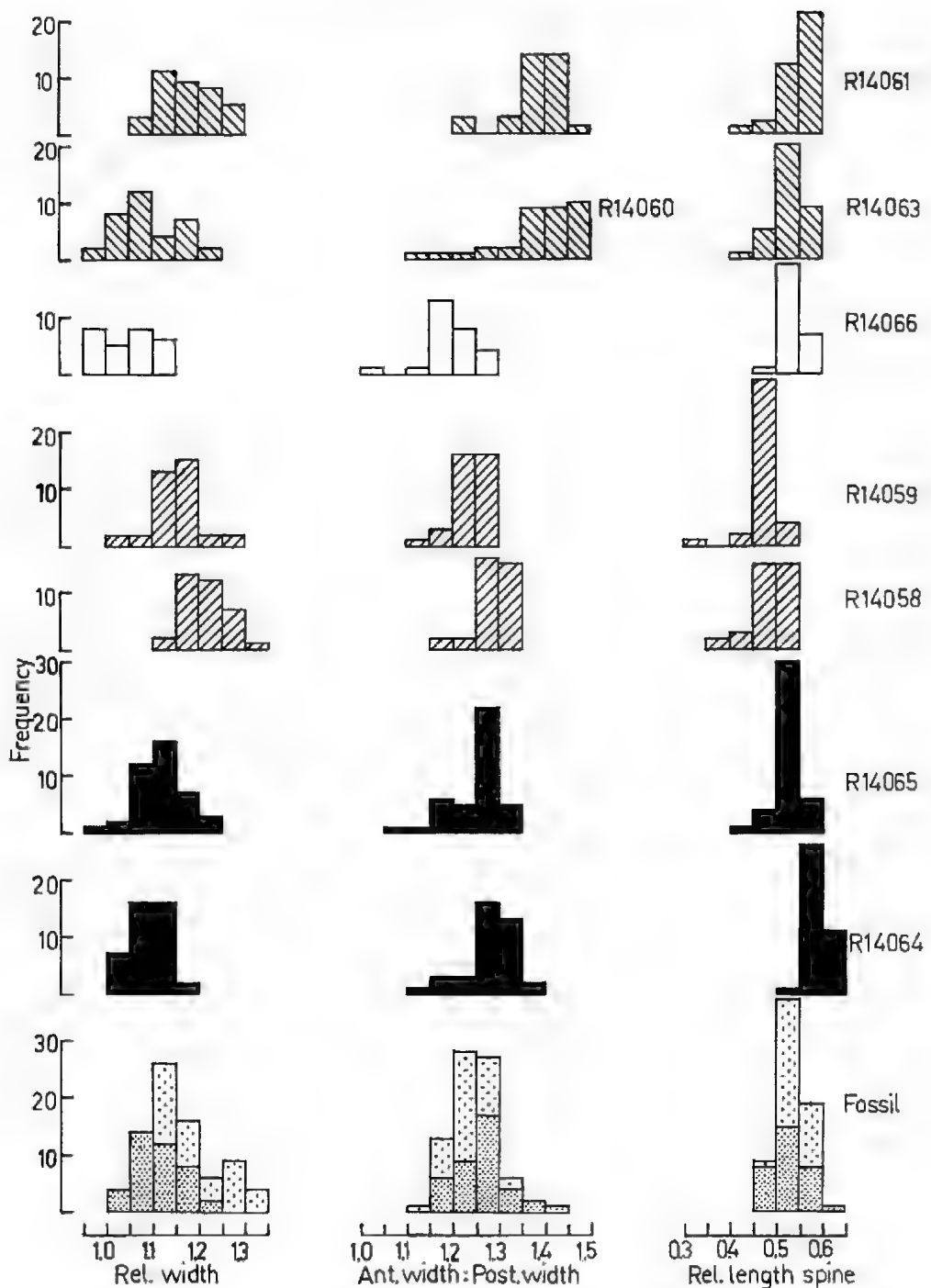


Fig. 3. Distributions of values for the ratios (a) width across postzygapophyses to length between zygapophyses, (b) width across accessory processes to width across postzygapophyses, and (c) minimum length of neural spine to length between zygapophyses. Left-to-right downward hatching, *Pseudechis porphyriacus*; open columns, *Austrelaps superba*; right-to-left downward hatching, *Notechis scutatus*; solid columns, *Pseudonaja nuchalis*; fine stipple, Victoria Cave, type A; coarse stipple, Victoria Cave, type B.

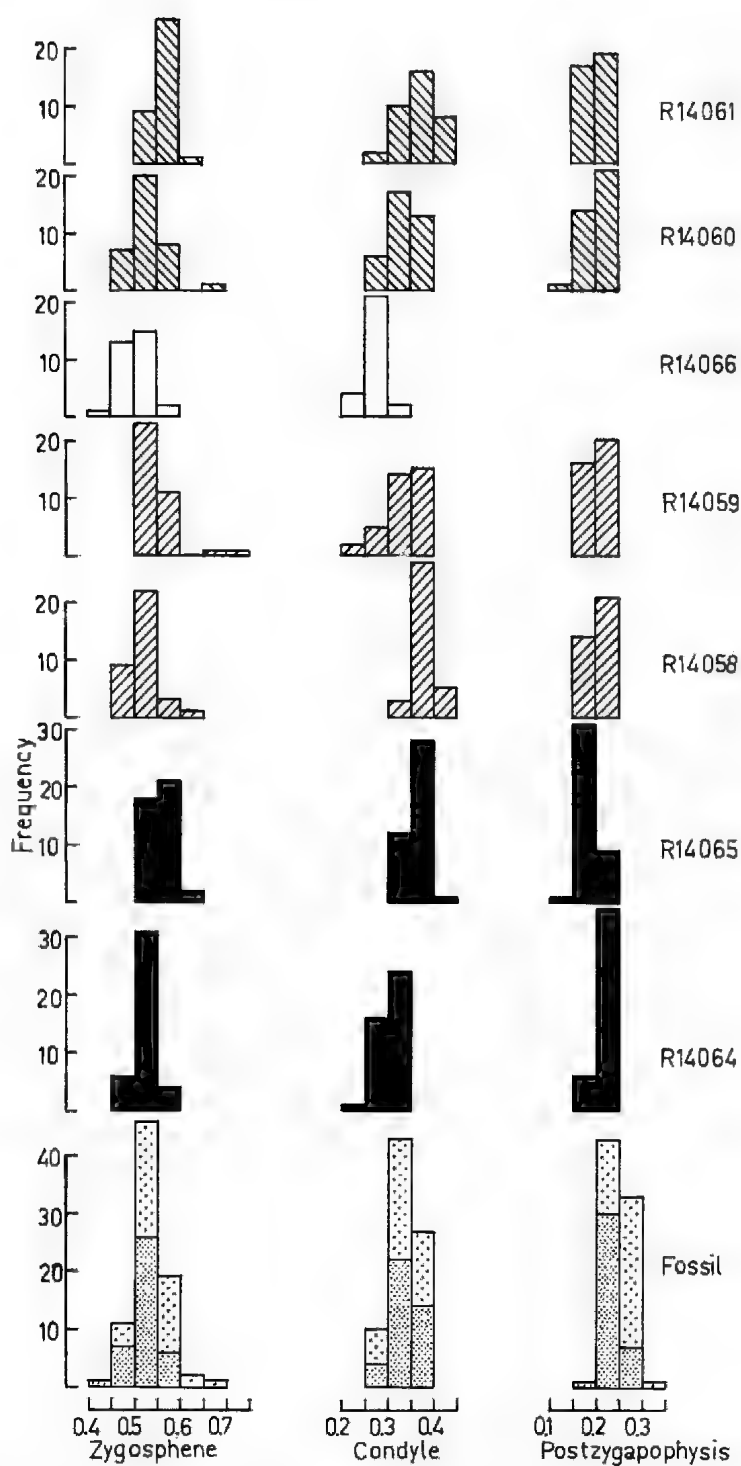


Fig. 4. Distributions of values for the ratios (a) width of zygosphere to length between zygapophyses, (b) width of condyle to length between zygapophyses, and (c) width of postzygapophysis to length between zygapophyses. Hatching as in Fig. 3.

TABLE 2

Some characteristics of the cloacal region of four specimens of *Pseustes porphyrius*

| Specimen | Total number of cloacal vertebrae | Number with articulated ribs | Number with single hypapophysis | Number with ribs deeply forked |
|----------|-----------------------------------|------------------------------|---------------------------------|--------------------------------|
| R14060 | 8 | 1 | 2 | 8 |
| R14061 | 5 | 1 | 3 | 5 |
| R14062 | 5 | 4 | 4 | 4* |
| R14063 | 6 | 2 | 3 | 5* |

* The anterior-most pair of ribs have shallow forks.

between zygapophyses [\bar{x} 0.33 \pm .0047 (36); \bar{x} 0.37 \pm .0067 (36)] (Fig. 4). The zygosphene, viewed from the front, is thin and straight or slightly convex; from above it is nearly straight or slightly concave with a faint median notch on some vertebrae. The width of the zygosphene is a little over half the length between the zygapophyses [\bar{x} 0.53 \pm .0063 (36); \bar{x} 0.57 \pm .0038 (35)]. The prezygapophysial facets are oblong [length/width 1.19–1.58, \bar{x} 1.40 \pm .019 (36); 1.01–1.73, \bar{x} 1.49 \pm .025 (36)]. The acute accessory processes extend laterally perpendicular to both vertical and horizontal axes of the vertebra, and project well beyond the articular facets. Hence the ratio of width across accessory processes to width across postzygapophyses is high [\bar{x} 1.39 \pm .014 (35); \bar{x} 1.38 \pm .010 (35)] (Fig. 3). The postzygapophyses are large [width postzygapophysis/length between zygapophyses: \bar{x} 0.20 \pm .003 (36); \bar{x} 0.20 \pm .002 (36)] and have an anterior notch that gives their otherwise ovate shape a kidney outline. The maximum diameter of the postzygapophysis is almost perpendicular to the long axis of the vertebra and exceeds the width [length/width 1.03–1.51, \bar{x} 1.27 \pm .020 (36); 1.02–1.46, \bar{x} 1.22 \pm .017 (36)].

The typical four pairs of foramina are present on all precloacal vertebrae, and in many vertebrae they are unilaterally or bilaterally doubled. For example, in the 183 precloacal vertebrae of R14061 the lateral foramina are bilaterally double (8 vertebrae), double on the right only (11) or left only (13); the paracotylar foramina are bilaterally double (1), double on the right only (5) or left only (8); the subcentral foramen is double on the right (2) or left (3) and in each of three vertebrae three pairs of subcentral foramina appear. A fifth pair of foramina is present in the precloacal vertebrae of all speci-

mens, each foramen of this pair opening through the accessory process near the anterolateral margin of the prezygapophysial facet.

Vertebral structure in the cloacal region varies widely between specimens, and the number of vertebrae with articulated forked ribs may be equal to or less than the number with a single hypapophysis (Table 2). The fork is deep on most forked ribs but on the most anterior cloacal vertebra, the notch may be midway along the rib. The lymphapophyses project laterally and slightly ventrally, as do the pleurapophyses of the post-cloacal vertebrae.

The haemapophyses of each post-cloacal vertebra arise separately from the ventral surface of the centrum, and remain completely separate, although on the anterior post-cloacal vertebrae the tips of the haemapophyses converge slightly. In lateral view the shape of the haemapophysis is similar to that of the hypapophyses of the precloacal vertebrae. The pleurapophyses are directed anterolaterally (viewed from above or below) and extend anterior to the cotyle.

Some irregularities occur in the skeletons. In R14060 the right prezygapophysial facets of the 130th to 134th vertebrae are enlarged to almost double the size of the left-side facet, and the right postzygapophyses of these vertebrae are slightly enlarged. A similar, but even greater, enlargement of the right prezygapophysis occurs in two vertebrae of R14062, where an outgrowth of spongy bone has completely fused the prezygapophysis to the preceding postzygapophysis, and the accessory process is reduced. These abnormalities probably resulted from injury, but R14063 shows slight congenital abnormalities, firstly on vertebra 91, where a small, but distinct epizygapophysial spine appears on the left side only, and secondly in four post-cloacal vertebrae. Near the beginning of the postcloacal series, the centra of two consecutive vertebrae are completely fused. On the left, the outline of the posterior edge of the neural arch of the first vertebra can be seen, but on the right the suture line is only faintly distinguishable. The pleurapophyses of both vertebrae lie close together, apparently fused to the centrum of the first vertebra. Two pairs of haemapophyses arise separately on the ventral surface of the combined centrum. Later in the post-cloacal series two vertebrae are more fully fused and share a common neural spine. Two pairs of haemapophyses are fused at their base near the condyle of the second vertebra. An apparently

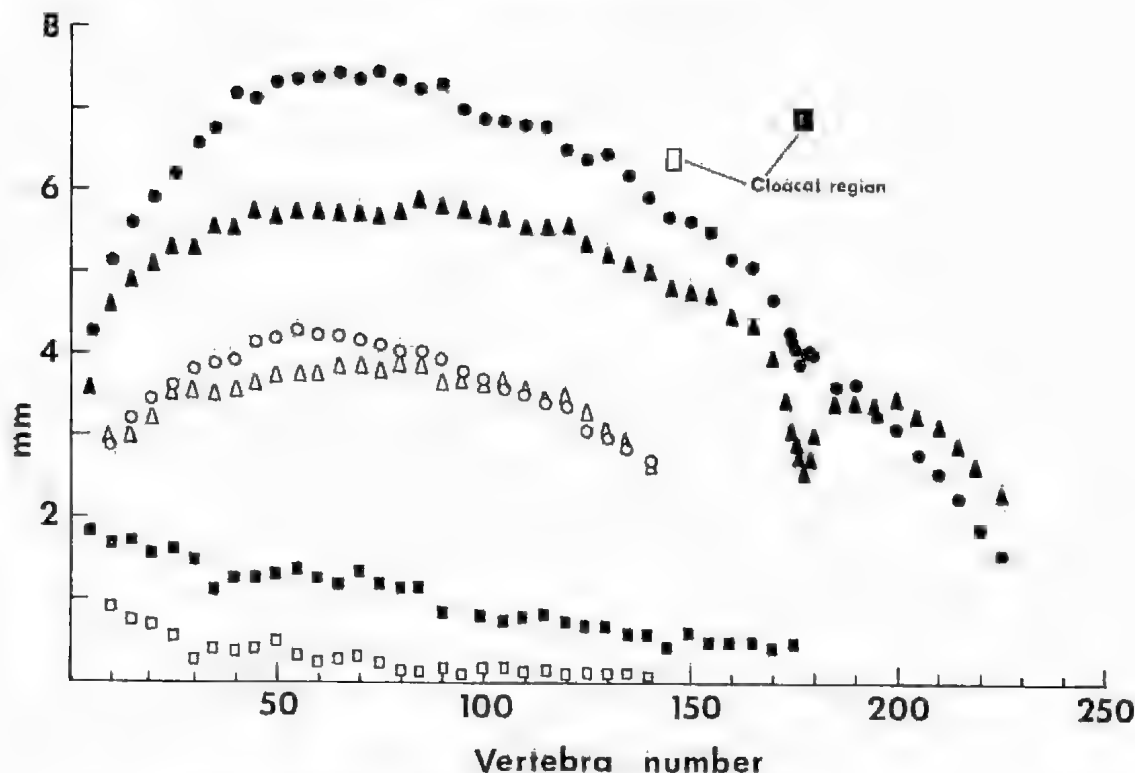


Fig. 5. Variation throughout the vertebral column in (a) length between zygapophyses (Δ \blacktriangle), (b) width across zygapophyses (\circ \bullet), and (c) length of hypapophysis (\square \blacksquare) in two species. Hollow symbols, *Austrelaps superba* (R14066), solid symbols, *Notechis scutatus* (R14058).

similar abnormality has been observed in dorsal vertebrae of colubrid snakes (King 1959).

Austrelaps superba (Günther)

The low number of precloacal vertebrae in this specimen (Table 1) is confirmed as typical of the species by the ventral scale number (151 according to Worrell 1963). The width across the postzygapophyses is less than the length between zygapophyses in the first ten and the last 35 precloacals (Fig. 3).

The hypapophysis (Fig. 5) is similar in form to that of *P. porphyriacus* and does not extend further posteriorly than the posterior surface of the condyle.

The subcentral ridges are low and rounded, as in *P. porphyriacus*, but the interzygapophyseal ridges of *A. superba* are stronger. Small epizygapophyseal spines occur on the first six vertebrae. The condyle is smaller, relative to the length between zygapophyses, than in *P. porphyriacus* (Fig. 4). The zygosphenes are thin and slightly convex from the front, convex

from above. The ratio of zygosphenes width to length between zygapophyses (Fig. 4) has a mean of $0.50 \pm .0038$ (27). The prezygapophyseal facets are oblong, the postzygapophyseal facets obovate. The acute accessory processes are relatively shorter than in *P. porphyriacus* in most vertebrae (Fig. 3).

Of the four cloacal vertebrae, one has articulated forked ribs and three have a hypapophysis. The haemapophyses of the post-cloacal vertebrae are long, anteroposteriorly, about half the length of the centrum, and are completely double.

Notechis scutatus (Peters)

In all precloacal vertebrae, the width across the postzygapophyses exceeds the length between zygapophyses (Fig. 5). Each hypapophysis is extremely compressed laterally to a thin lamella that terminates posteriorly in a sharp point not extending posterior to the posterior surface of the condyle in any but the first 15 vertebrae, where the hypapophysis is

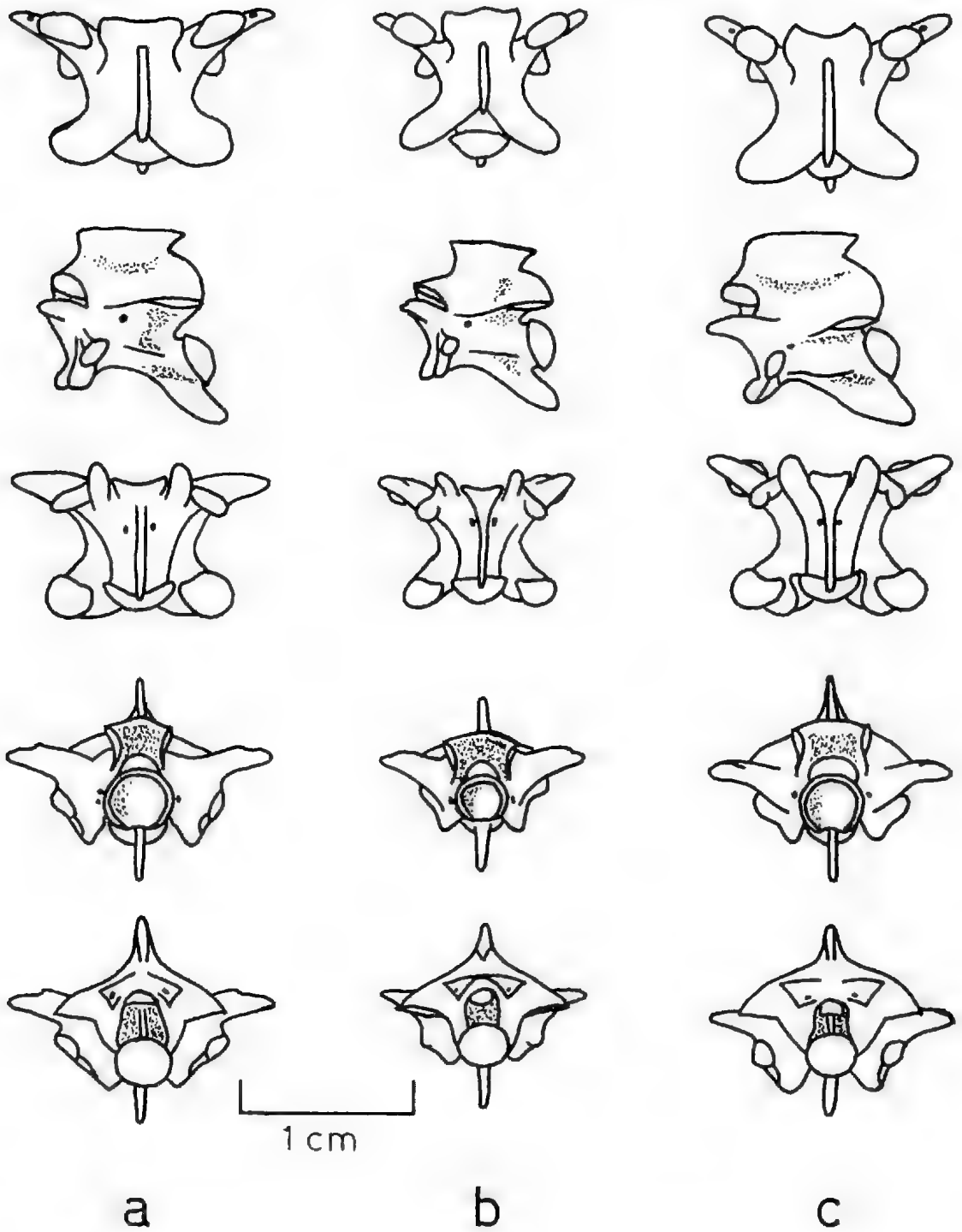


Fig. 6. Line drawings, to exact scale, of the 80th vertebra of (a) *Pseudechis porphyriacus* (R14060), (b) *Notechis scutatus* (R14059), and (c) *Pseudonaja nuchalis* (R14064) in dorsal, lateral, ventral, anterior and posterior views.

very long (Fig. 5). The subcentral ridges are low and rounded; the interzygapophysial ridges are weak but distinct. The neural spine is higher than in *P. porphyriacus* (Fig. 6) and its horizontal dorsal edge overhangs both anteriorly and posteriorly. The minimum length of the neural spine is generally relatively shorter than in the specimens of *P. porphyriacus* [ratio of minimum length of neural spine to length between zygapophyses: \bar{x} 0.48 \pm .0064 (35); \bar{x} 0.48 \pm .0049 (36)] (Fig. 3). Epizygapophysial spines are well developed on the first four vertebrae, faintly distinguishable on the fifth to eighth, but absent from all others.

The round condyle is set on a short but distinct neck (Fig. 6). The thin zygosphenoid is straight or slightly convex from the front, straight or slightly concave from above. The prezygapophysial facets are oblong [length/width 1.00–1.67, \bar{x} 1.47 \pm .027 (35); 1.09–1.58, \bar{x} 1.35 \pm .022 (35)]. The accessory processes are obtuse and short, so that the ratio of width across accessory processes to width across postzygapophyses is generally less than in *P. porphyriacus* (Fig. 3). The postzygapophyses are obovate [length/width 1.10–1.58, \bar{x} 1.35 \pm .021 (35); 1.00–1.47, \bar{x} 1.28 \pm .022 (35)], and their width is about one-fifth of the length between the zygapophyses (Fig. 4). Prezygapophysial foramina are constantly present.

In both specimens, all five cloacal vertebrae have fused forked ribs. One has three, the other two cloacal vertebrae with a single hypapophysis.

The haemapophyses are large, paddle-shaped and completely paired. The pleurapophyses extend ventrally more than laterally. The zygapophysial facets extend anteriorly and posteriorly, rather than laterally as in the pre-cloacal vertebrae, and acute accessory processes are distinct on all the postcloacal vertebrae.

Unilateral or bilateral doubling of the paracotylar and/or subcentral foramina occurs in a very few pre-cloacal vertebrae (no more than four in either specimen).

Pseudonaja nuchalis Günther

Pseudonaja nuchalis has more vertebrae than any of the other species studied here (Table 1), and maximum length and width occur in sequentially more posterior vertebrae than in the other species (Fig. 7). All pre-cloacal vertebrae are wider than long. The

hypapophysis is well developed on all pre-cloacal vertebrae. Thickenings on the rim of the cotyle on either side of the ventral midline give rise to a low ridge that narrows sharply to join the laterally-compressed hypapophysis. The hypapophysis deepens from about the middle of the vertebra and terminates in a rounded point that extends posteriorly to the condyle. Subcentral ridges are strong and interzygapophysial ridges are distinct. The paradiapophyses are well developed, with a protruding, dorsoventrally-elongated upper facet and saddle-shaped lower facet. The parapophysial processes appear in ventral view as a flat surface nearly as broad as long; the ventral projection of these processes is medial to the lateral border of the cotyle. The neural spine is low and long (Figs 3 and 6); its dorsal edge overhangs slightly at the front, markedly behind. Epizygapophysial spines are distinct on the first five vertebrae, faintly visible on the sixth to eighth and absent from all others. The cotyles and condyles are almost round; in R14065 some cotyles are depressed slightly, but in R14064 some are slightly compressed laterally. The condyles are relatively much larger in the smaller specimen than in the larger one (Fig. 4). The zygosphenoid is convex from the front, concave from above; it is thin in vertebrae of the smaller specimen but is thickened in those of the larger. The prezygapophysial facets are oblong [length/width 1.09–1.72, \bar{x} 1.39 \pm .022 (41); 1.18–1.78, \bar{x} 1.35 \pm .018 (41)], and the acute accessory processes extend laterally well beyond the articular facets (Fig. 3). Except for a slight notch posteriorly, the outline of the postzygapophysial facet is almost round [length/width 1.03–1.35, \bar{x} 1.17 \pm .011 (41); 1.09–1.59, \bar{x} 1.30 \pm .019 (41)].

In the cloacal region the ribs are all fused except for the anterior vertebra of R14064, and a hypapophysis occurs on one (R14065) or three (R14064) cloacal vertebrae.

The haemapophyses are completely paired and extend anteriorly as two separate ridges to the rim of the cotyle. The pleurapophyses are broad and flat and not pointed. In anterior view they project ventrolaterally but in ventral view mainly laterally and only slightly anteriorly.

In R14065, more than the one pair of paracotylar foramina appear on many vertebrae—15 pre-cloacal vertebrae have an extra paracotylar foramen on the right side, 18 on the left and 34 on both sides. R14064 has only

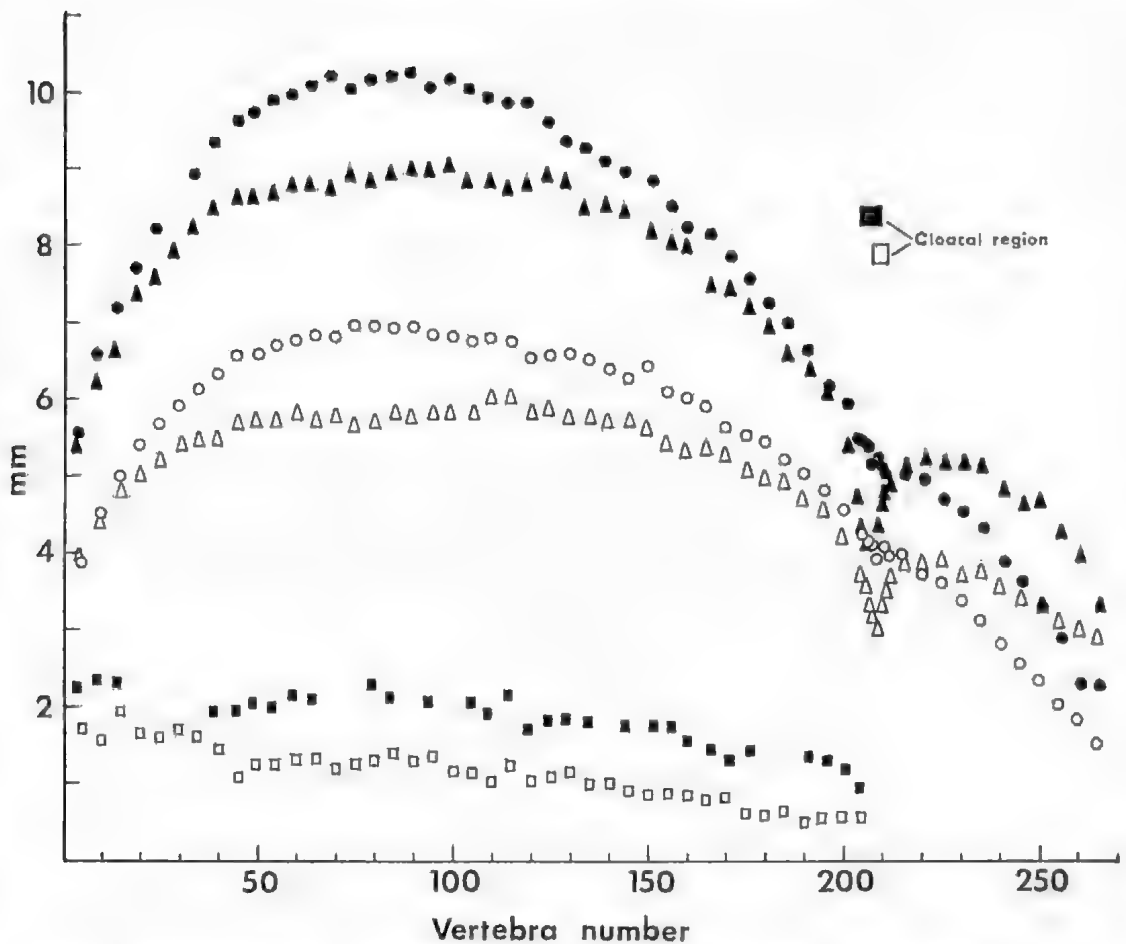


Fig. 7. Variation throughout the vertebral column in (a) length between zygapophyses ($\triangle \blacktriangle$), (b) width across zygapophyses ($\bigcirc \bullet$), and (c) length of hypapophysis ($\square \blacksquare$) in *Pseudonaja nuchalis*. Solid symbols, R14064, hollow symbols, R14065.

8 precloacal vertebrae with additional paracotylar foramina. The left postzygapophysis of the 114th vertebra is fused by an outgrowth of spongy bone to the prezygapophysis of the succeeding vertebra, which lacks an accessory process on the left side. The left rib of vertebra 114 shows a healed fracture near the articulation with the vertebra.

Pleistocene fossil vertebrae from Victoria Cave

The precloacal vertebrae found in the Victoria Cave deposit vary in length from about 2 mm to a maximum length between zygapophyses of 11.1 mm. In their general conformation they closely resemble those of *Pseudonaja*. However within the sample of vertebrae from Victoria Cave, two types can be distinguished on the characteristics of the zygosphenes: Type A; slightly convex when viewed from above,

convex in anterior view and slightly thickened; Type B; almost straight, with a median notch, when viewed from above, almost straight in anterior view and extremely thickened. This thickening is consistent with the robust appearance of the vertebrae. The subcentral ridges are particularly strong (Fig. 8).

As well as the thickening of the zygosphenes, its width relative to the length between zygapophyses differs significantly between the types A and B [A, \bar{x} $0.52 \pm .0048$ (40); B, \bar{x} $0.54 \pm .0057$ (40); $.002 < P < .01$]. The distributions of the values for this ratio overlap widely not only between types A and B from Victoria Cave but also among the specimens studied (Fig. 4). The ratio of width across postzygapophyses to length between zygapophyses tends to be greater in the fossil vertebrae than in *A. superba*; the ratio of width

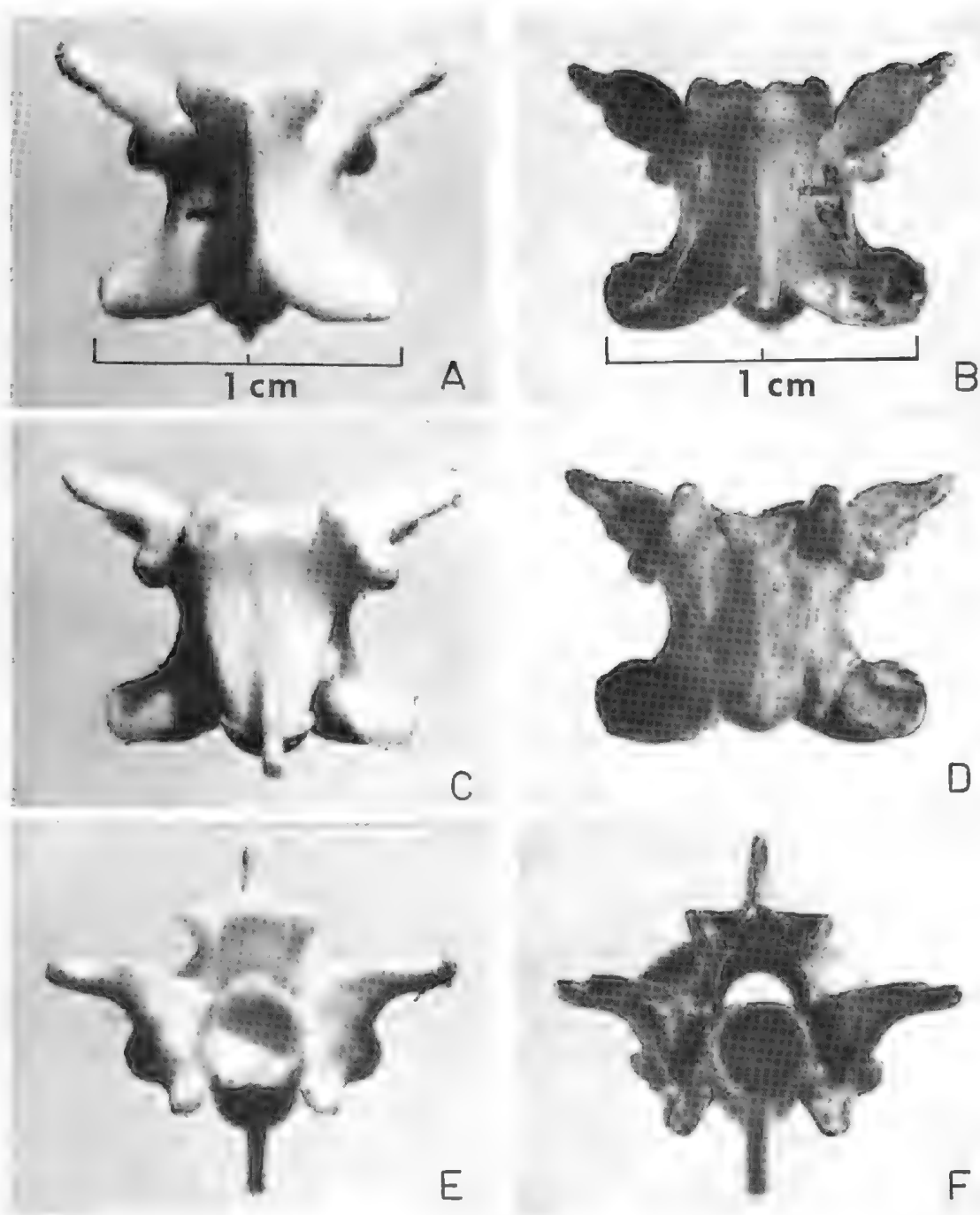


Fig. 8. Preloacal vertebrae of *Pseudonaja nuchalis*; left, 80th preloacal of R14064; right, Victoria Cave, Type B (P16126b) in dorsal (A, B), ventral (C, D) and anterior (E, F) views.

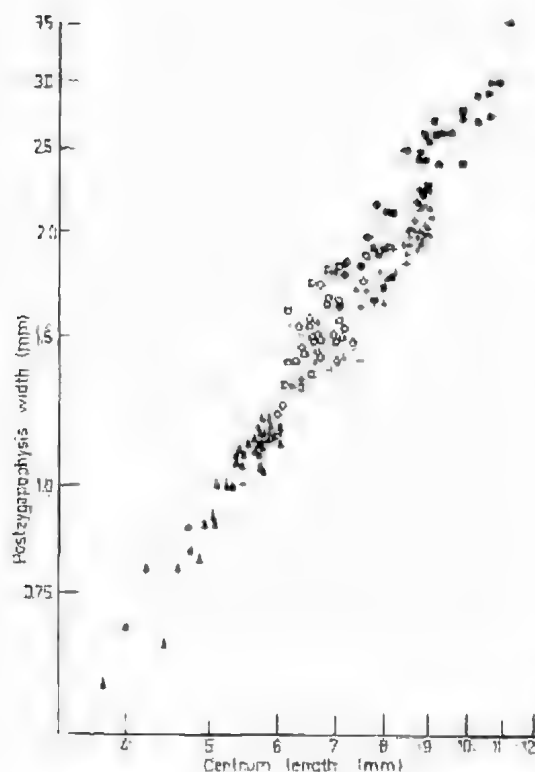


Fig. 9. Double-logarithmic regression of width of postzygapophysis on length between postzygapophyses in *Pseudonaja nuchalis*, Δ , R14054; +, R14064; \circ , fossil, Type A; \bullet , fossil, Type B.

across accessory processes to width across postzygapophyses is less than in most *P. porphyriacus* and the relative length of the neural spine is generally greater than in *N. scutatus* (Fig. 3). In these ratios, the Victoria Cave vertebrae closely resemble *P. nuchalis*. In the relative width of the condyle, the distribution of ratios for Victoria Cave vertebrae resembles the larger *P. nuchalis* (R14064), though not the smaller (R14065). Finally, in the relative width of the postzygapophyses the Victoria Cave vertebrae of Type A resemble the larger but not the smaller *P. nuchalis*, and the relative width of the postzygapophysis is generally greater in Type B fossils than in any of the modern species studied (Fig. 4).

This subjective and objective analysis of the fossil vertebrae indicates that they most closely resemble *Pseudonaja*. The Type A vertebrae can be referred with confidence to this genus. Because the Type B vertebrae differ in the thick zygosphenes and the relatively large post-

zygapophyses, the possibility exists that they are of a species different from Type A. However, these characteristics are two which develop with age (Auftenberg 1963) and most of the Type B vertebrae are larger than the Type A (Type A, length 6.0–8.1, \bar{x} 6.7; Type B, 7.1–11.1, \bar{x} 8.9) and also generally are larger than the vertebrae of the modern specimens. When the correlation between length between zygapophyses and relative width of postzygapophysis of Type B vertebrae was tested by the Kendall Rank Correlation Test (Siegel 1956) the correlation was found to be highly significant ($\tau = 0.41$, $z = 3.765$, $P < .001$). On a double-logarithmic plot of postzygapophysis width against length between zygapophyses, the distribution of values for the fossil vertebrae (of both types, A and B) falls near the same straight line as those of R14064 and R14065 (Fig. 9). The similarities between Victoria Cave preloacal vertebrae and those of modern *P. nuchalis* so far outweigh the slight differences that recognition of the fossils as a separate species seems unnecessary at least until the limits of variations of modern species are better known.

The post-cloacal vertebrae recovered from Victoria Cave resemble those of *P. nuchalis* in the laterally-directed pleurapophyses. In the other species studied the pleurapophyses project anterolaterally.

Discussion

In all the vertebrae of the four species, the hypapophysis is well-developed (as in all elapids) and hypapophysis length decreases slowly from anterior to posterior along the column. There is no suggestion of two distinct regions as in *Achrochordus javanicus* where the anterior region (to vertebra 96) has hypapophyses long and fairly constant in length and the posterior region has hypapophyses short and of constant length (Hoffstetter & Gayard 1964).

At family level, the presence of vertebral foramina may have diagnostic value [e.g. the constant absence of lateral foramina in *Achrochordidae* (Hoffstetter & Gayard 1964)], but the variability in the number of foramina at each position (i.e. lateral, subcentral, etc.) in the one snake indicates the need for caution in the use of foramina in taxonomy.

Although middle precaudal vertebrae may be the most constant in their structure (within species) and hence best for identification

(Auffenberg 1963), the difficulty of assigning an isolated elapid vertebra to a particular region of the column precludes confidence in selecting middle precaudals from a sample of fossils. Because of the consistent variations along the column, together with some irregular variation (e.g. doubling of foramina), to identify isolated vertebrae it is necessary to consider not just the middle precaudal vertebrae of reference specimens, nor the mean of some value (even if it be given with standard error) but the range through which a given character varies. Also because of variations along the column, no unique specific character was found, and so it is necessary to consider several characters in the identification of fossils. The

fossil genera may be readily identified, but further studies of congeneric species are needed to determine whether specific identification is possible.

Acknowledgments

Mr R. Shine, Mr G. Whitten and Dr R. T. Wells kindly donated the modern snakes. Dr Wells and members of the Cave Exploration Group of South Australia helped in excavating the fossil vertebrae. I am grateful to Dr R. T. Wells, Mr I. M. Thomas, Dr T. F. Houston and Mr N. Pledge for their criticisms of the manuscript. Mr P. Kempster prepared the photographs for Fig. 8.

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THE ONTOGENY OF THE VOCAL SAC OF THE AUSTRALIAN LEPTODACTYLID FROG, *LIMNODYNASTES TASMANIENSIS*

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Summary

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The ontogeny of the vocal sac of *Limnodynastes tasmaniensis* proceeds from initial bilateral evaginations of the mouth floor, through median fusion to a unilobular, submandibular structure. The acquisition of pigmentation by the submandibular skin is a concomitant process. It is suggested that the vocal sac evolved by a path now reflected by ontogeny, and involving progressive bilateral herniation.

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Introduction

Vocal sacs occur only in male anurans and, in most species, comprise inflatable, epithelium-lined chambers located between the hyoid plate and the superficial mandibular musculature. Data on the ontogeny of vocal sacs are limited to studies on only a few, mostly African, species (Inger 1956; Inger & Greenberg 1956). The available information is so inadequate that the possible contribution of ontogeny to an understanding of the evolution of vocal sacs has not been assessed. At present there is no published information on the ontogeny of the vocal sacs of any of the 300 (approx.) species of frogs found in Australia and New Guinea.

The Australian leptodactylid species *Limnodynastes tasmaniensis* represents an ideal initial subject for studies of vocal sac ontogeny. This is because the superficial mandibular musculature of adults has already been described in detail, and there are published observations on variation in the position occupied by the vocal sac when it is inflated (Tyler 1971).

Material and Methods

Of 646 specimens of *Limnodynastes tasmaniensis* in the South Australian Museum, one series was found to exhibit ontogenetic variation in the extent to which the vocal sac intrudes above the superficial mandibular musculature. This series comprises 18 male specimens from a group of 68 males collected at

West Beach near Adelaide on 1 September 1963 (SAM, R5290). The snout to vent length of the 18 males ranges from 30 to 34 mm.

Dissections were performed with the aid of a low-power binocular microscope, and measurements made with a pair of dial calipers. The muscles were stained with the reversible iodine/potassium iodide stain described by Bock & Shear (1972), in order to differentiate the vocal sac from the surrounding striated muscles. Muscle and vocal sac terminology follow that of Tyler (1971).

Observations

Secondary Sexual Characteristics

The secondary sexual characteristics of *Limnodynastes tasmaniensis* are as follows: males possess a unilobular, submandibular vocal sac, yellow pigmentation of the submandibular skin and glandular nuptial pads on the first and second fingers. Females bear broad lateral fringes to the first and second fingers, and sometimes to the third.

Vocal Sac Ontogeny

The earliest step in the progress towards the development of vocal sacs involves the formation of a shallow and elongate involution of the floor of the mouth on one side of the tongue. There is a slight elliptical, ventral depression with a mediad inclination (Fig. 1A), and the lateral margin of the depression is level with the lateral border of the anterior cornu of the hyoid.

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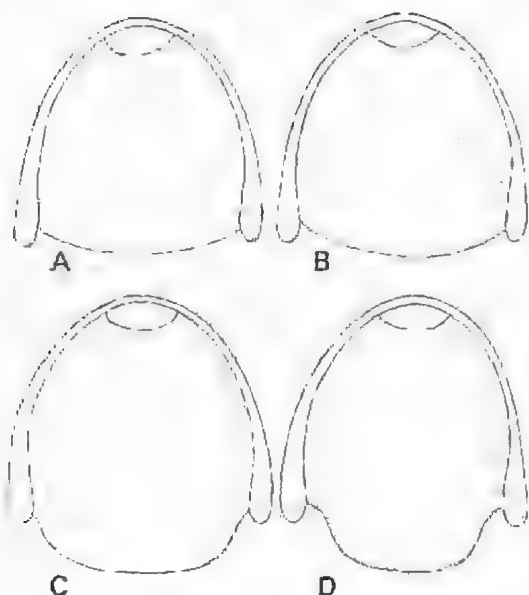


Fig. 1. Selected progressive stages in ontogeny of vocal sac. A. Single, elliptic ventral depression. B. Bilateral expansion mediad. C. Further mediad and initial caudad development. D. Medial unity of separate sacs.

In four specimens, development was confined to such an evagination on the left side; in a fifth there were bilateral evaginations. From these slight folds the vocal sac develops bilaterally, and as far as could be determined quite concomitantly, into roughly circular bags intruding between the superficial, ventral, mandibular musculature and the deep intermandibular muscles situated above them (Fig. 1B). At this stage of progress mediad development is more pronounced than anterior or posterior development. Simultaneously, that area of the mouth floor between the anterior cornu and the mandible becomes depressed, rendering the aperture to each portion of the sac more conspicuous.

As the two halves of the vocal sac approach one another, their posterior margins extend further caudad (Fig. 1C). This posterior enlargement is accompanied by comparable enlargement of the interhyoideus muscle into a slight lobe, extending beyond the post-articular extremities of the mandibles. Ultimately the vocal sac occupies the entire muscular lobe, becoming united medially by loss of the common medial wall (Fig. 1D).

The presence and extent of submandibular dermal pigmentation was found to provide an

accurate external index of the presence, and stage of development, of the vocal sac structure. In specimens lacking the initial evaginations in the mouth floor, the submandibular skin was either entirely unpigmented or else bore a few scattered chromatophores at the periphery of the mandibles. Development of the evaginations was accompanied by an increase in the density of pigmentation and of its medial limit. The pigmentation, and the appearance of the bright yellowish background color of the submandibular skin, progressed in an identical sequence until, at completion of vocal sac development, the skin was entirely yellow.

Discussion

Beyond the sphere of its intrinsic interest, ontogeny can contribute to an understanding of the evolution of structure. In the present situation the progression of the vocal sac from paired, lateral evaginations to a single, large sac could readily be regarded as a recapitulation of evolutionary history. However, the nature of the progression also indicates why the anuran vocal sac originates in the way that it does.

The floor of the mouth is supported by the hyoid plate and its processes, and by muscles communicating between the hyoid and the mandibles. These supporting structures provide what can be visualised as a broad and complex sling in which the only gaps are a narrow lateral zone on each side of the tongue, so situated between the anterior cornua and the mandibles. In all anurans possessing vocal sacs, apertures originate within these 'unsupported' zones.

The probable steps that lead to the evolution of vocal sacs in this species, or its ancestral stock, can be reconstructed quite readily. Assuming an increase in the pressure of the buccal cavity during vocal activity, the existing sites of the vocal sac apertures are probably the areas of least resistance: in these regions the superficial tissue is of a rather elastic nature, and presumably subject to the greatest distension. It follows that the first stage in the ontogeny of the vocal sac of *Limnodynastes tasmaniensis* is precisely that initial event. Subsequent stages could well have arisen from little more than progressive bilateral herniation.

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THE PRE-SETTLEMENT VEGETATION OF THE MT GAMBIER AREA, SOUTH AUSTRALIA

*BY R. J. DODSON**

Summary

DODSON, J. R. (1975).-The Pre-Settlement Vegetation of the Mt Gambier area, South Australia.
Trans. R. Soc. S. Aust. **99**(2), 89-92, 31 May, 1975.

There are some conflicts as to the nature of the pre-settlement vegetation formations around Mt Gambier and Glencoe. European settlers long ago cleared the areas of their vegetation cover. Pollen analysis of Brownes Lake sediment reveals that the most likely formation around Mt Gambier consisted of open grassland with perhaps a sparse cover of woody taxa.

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Pollen analysis of Brownes Lake sediment reveals that the most likely formation around Mt Gambier consisted of open grassland with perhaps a sparse cover of woody taxa.

Introduction

Crocker (1944) left gaps in his vegetation map in the areas around Mt Gambier and Glencoe, in south-eastern South Australia, as the original vegetation was no longer evident at the time of his survey. Crocker (1944) and Tiver & Crocker (1951) hypothesized that the areas were occupied by lightly wooded grassland, and the trees cleared after settlement. Woods (1862) recorded the vegetation in the Blue Lake crater at Mt Gambier as thickly wooded with several varieties of *Melaleuca*. The vegetation is sparse in the photograph in Hill (1972, p. 108) taken in 1860 and yet Hill when describing an early record (1861) of the first road between Mt Gambier (then Gambiertown) and Port McDonnell on the coast states (p. 109)

"the route to the 'Bay' was through dense bush country, mud and slush in winter, dust in summer, and tenanted by thousands of kangaroos at all times."

Specht (1972, p. 203) in his vegetation map of the South East simply records the areas around Mt Gambier and Glencoe as cleared.

Brownes Lake occupies portion of one of the craters which formed in the volcanic eruptions at Mt Gambier after 5000 years B.P. (Fergusson & Rafter 1957, Blackburn 1966). It is 4-5 m deep, sits on collapsed volcanic debris and its water surface, like those of the other three crater lakes, is an expression of the regional water table (Bayly & Williams 1964,

1966). Hill (1972) recounts some of the early records of water level changes of the Mt Gambier lakes and it appears that the most spectacular observed were in Brownes and Leg of Mutton Lakes. These are the shallowest and thus changes may have been more obvious. Henty's hut, the first building in the area, is said to have been erected in 1841 on the site of Brownes Lake. Brownes Lake and Valley Lake filled and joined and the new lake reached its maximum depth in the 1890's.

This paper provides data on early vegetation at Mt Gambier. Pollen analysis is an ideal method for tackling this problem as the crater walls are mostly steep-sided and can support little local vegetation. Therefore a significant proportion of the pollen rain is probably regionally derived. Today the craters are heavily exploited for recreation purposes and most of the vegetation within them is introduced. The change from native vegetation should be recorded in the fossil pollen record.

Methods

Before the Brownes Lake core site was selected for investigation, areas of Brownes Lake, Valley Lake and Leg of Mutton Lake were checked for undisturbed sediment. Access to sediment at Blue Lake was impossible with the equipment at hand. A 160 cm sample of peat was collected from Leg of Mutton Lake. The dry periods in Leg of Mutton Lake (Hill 1972, pp. 112-114) which are unfavourable for pollen preservation rendered this core un-

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POLLEN SUM : TOTAL TERRESTRIAL POLLEN (excluding PINUS + PLANTAGO)

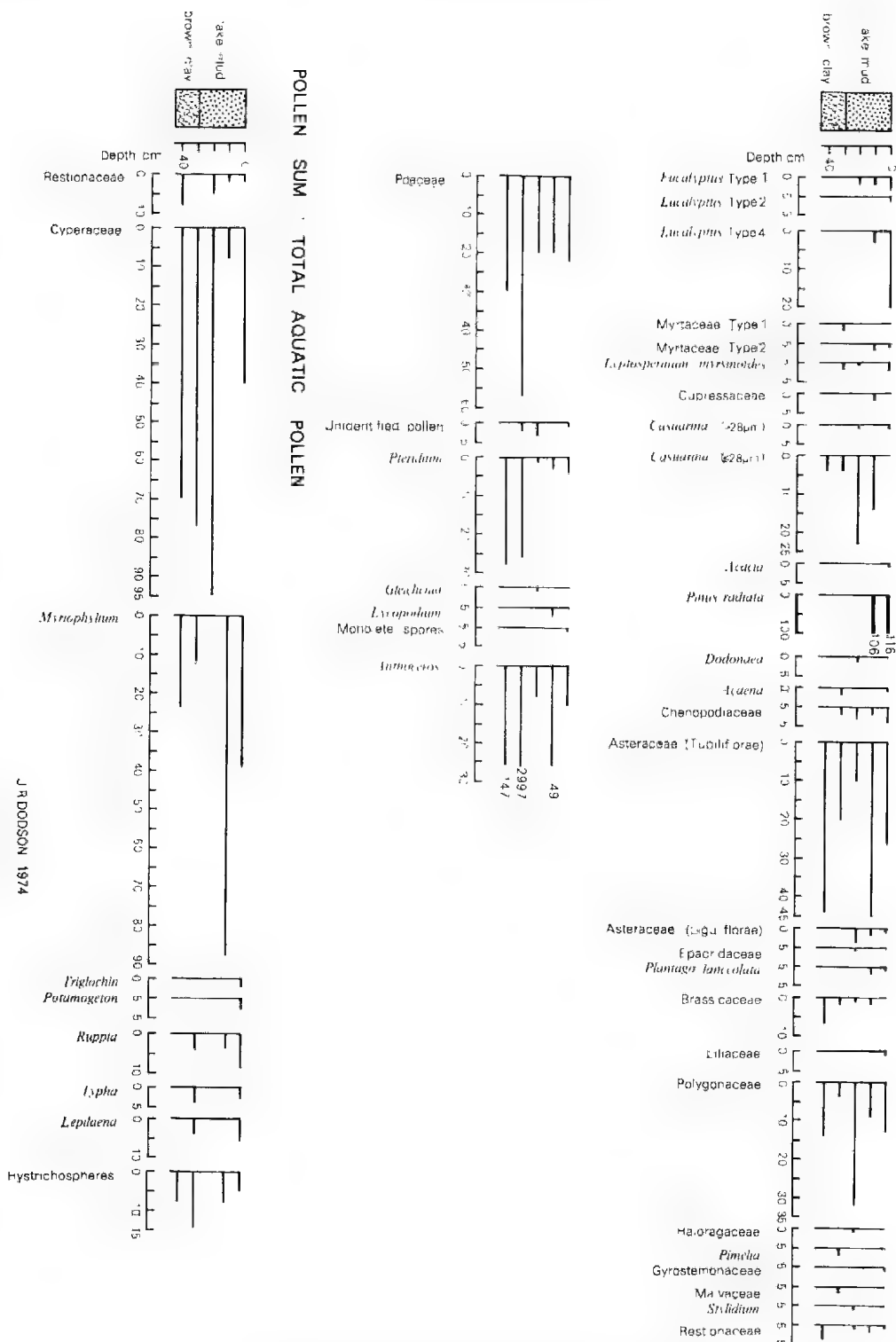


Fig. 1. Pollen diagram for Brownes Lake.

suitable for pollen analysis. No suitable sites were found at the accessible areas in Valley Lake nor in much of the Brownes Lake area.

In February 1974, a 45 cm core was collected with a D-section sampler from the core site on the eastern shore of Brownes Lake. It consisted of 30 cm of black lake mud overlying 15 cm of pale brown (straw coloured) material which was largely clay-sized particles of silica. This is probably reworked volcanic debris. The core was sampled on-site and pollen analysis was carried out in the laboratory using the standard hydrofluoric acid, alkali and Erdtman's acetylosis methods as described by Faegri & Iversen (1964). Residues containing pollen were dehydrated, mounted in silicone oil, and counted until at least 200 pollen grains of woody taxa had been recorded. Relative percentages for terrestrial pollen and spore taxa were calculated against a pollen sum of total land plant pollen excluding the recorded introduced taxa (*Pinus* and *Plantago lanceolata*). Frequencies for aquatic vascular plant pollen and Hystrichosphere remains were calculated against a pollen sum of total aquatic pollen. The results were plotted on a pollen diagram (Fig. 1). Ecological information for taxa in the study area and details of pollen identification have been given by Dodson (1974).

Results and Discussion

The short pollen diagram (Fig. 1) has not been divided into zones, but the presence of introduced taxa divides the diagram into post-settlement (0–10 cms) and pre-settlement phases (20–45 cms).

The pre-settlement phase was dominated by Asteraceae (Tubuliflorae), Poaceae and Pteridium, with small numbers of herb pollen. Tree pollen was virtually absent, although small and increasing frequencies of scrub taxa (*Casuarina* ($\leq 28\mu\text{m}$)—probably *C. paludosa*, and Myrtaceae Type 1—*Leptospermum juniperinum* and *Leptospermum myrsinoides*) were obtained. Assuming that regional pollen dominates, then the assemblage most likely represents open (treeless) vegetation in the

region with a heath fringe around the lake. The local vegetation was mainly *Anthoceros*, Cyperaceae, and *Myriophyllum*, representing a shallow water environment at the core site. This pollen assemblage tends to confirm the Crocker hypothesis that trees were few, rather than the early report recounted by Hill, unless the scrub described by the latter consisted of low pollen producers such as *Banksia* or *Acacia*. There is no evidence in the form of remnant vegetation to support this. The organic and pollen and spore content of the sediment was low (except for *Anthoceros* spores which must have been derived locally), suggesting either slow sedimentation during alternating wet and dry conditions (which could result in the loss of pollen through oxidation) or fairly rapid in-wash of inorganic material from the steep crater walls. On the evidence presented here it is not possible to favour either explanation.

The post-settlement phase of the pollen diagram is dominated by Poaceae, herbs and *Pinus radiata*, and also shows increasing *Eucalyptus* frequencies. *Anthoceros* and Cyperaceae decrease in importance and *Myriophyllum* dominates the aquatic spectra, indicating a change to deeper water at the core site. Since the core site is near the edge of the lake, it follows that water would not be deep there until the level rose above its present position. Since the rise accompanies the increase in pollen of exotic plants, it seems likely that the rise is the one recorded for the latter part of the 19th Century when Brownes Lake and Valley Lake were joined. The increase in *Eucalyptus* pollen is undoubtedly due to the plantings established in the craters for recreation facilities and the wildlife reserve and not to any change in the native vegetation.

Acknowledgments

It is a pleasure to thank Gurdip Singh and Joan Guppy who critically read the manuscript, and the Australian National University for supporting the work with finance and equipment.

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AUSTRALIAN LEPTODACTYLID FROGS OF THE *CYCLORANA AUSTRALIS* COMPLEX

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Summary

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Cyclorana australis as now defined is shown to comprise two closely related species: *C. australis* confined to northern Australia and *C. novaehollandiae* to eastern Australia. Notes are provided on the tadpole of *C. australis*, and the calls of both species are analysed. Call divergence is so limited that hybridization is considered possible in sympatry.

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Introduction

In recent years, examination of the biology and morphology of several geographically widespread "species" of Australian frogs has revealed that each comprises a complex of species. For example, *Crinia signifera* as recognised by Parker (1940) is now known to be a complex of seven species (Moore 1954; Littlejohn 1957; Main 1957; Straughan & Main 1966; Tyler & Parker 1974); *Mixophyes fasciolatus* is now four species (Straughan 1968) and *Limnodynastes dorsalis* is also four (Martin 1972).

The most neglected leptodactylid genus is *Cyclorana*, of which the type species is *Alytes australis* Gray (1842), described from material collected in the Northern Territory. This species, as currently defined, extends from northern Western Australia to northern New South Wales: a geographic range of approximately 3500 km. The conspecificity of individuals from the extremes of this extensive range is obviously suspect, and even the most cursory comparison of specimens of *C. australis* from the Northern Territory and northern Western Australia with those from Queensland reveals striking differences between them. The northern individuals tend to have a rather elongated head, a distinct, dark rostral stripe and a narrow subocular bar. In contrast, most individuals from Queensland are particularly robust animals with a broad head, and frequently obscure head markings: a population described as *Cyclorana nova-*

hollandiae by Steindachner (1867), and as *Phractops alutaceus* by Peters (1867). Both names were referred to the synonymy of *australis* by Boulenger (1882).

We have assembled and examined large collections of *C. australis* (*sensu lato*) from various sources. Here we report our findings and propose the recognition of a complex of two species.

Methods

The specimens reported are deposited in the following institutions: National Museum of Victoria (NMV); Naturhistoriska Riksmuseet, Stockholm (NR); Department of Zoology, University of Melbourne (MUZD); Northern Territory Museum, Alice Springs (NTM); Queensland Museum (QM); South Australian Museum (SAM); and Western Australian Museum (WAM).

Measurements of specimens (to 0.1 mm) were obtained with a pair of Helios dial callipers. Abbreviations employed in the text and tables are as follows: F = foot length (the distance between the proximal end of the tarsus and the distal tip of the fourth toe); HL = head length (the distance between the anterior extremity of the snout and the posterior margin of the tympanic annulus); HW = head width (the maximum width of the head, usually taken at the posterior extremity of the mandibles); TL = tibia length (obtained by placing the tibia between the callipers); S-V = snout to vent length (the distance between

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the anterior tip of the snout and the anterior margin of the cloaca).

Ratios calculated and subjected to the Student *t*-test were TL/S-V, HL/HW, F/S-V, F/TL and S-V/HW. Larval stage numbers follow those employed by Gosner (1960).

Mating calls were recorded in the field using a Uher 4000 Report portable tape recorder and Beyer M69 dynamic microphone, at a tape speed of 19 cm/sec. Calls were analysed by use of a sound spectrograph (Kay Model 6061-A Sona-Graph) with the overall response curve maintained in the FL-1 position. Three calls of each individual were analysed and mean values calculated. Each call was analysed twice; a narrow-band (45 Hz band-pass) analysis at recording speed to determine duration and dominant frequency, and a wide-band (300 Hz band-pass) analysis at half recording speed to resolve fundamental frequency.

The *Cyclorana australis* complex

Frogs of the *Cyclorana australis* complex are relatively large animals; the snout to vent length of adult males ranges from 61.4 to 81.4 mm, and that of females from 69.9 to 102 mm. They are all generally robust with a broad and frequently bloated body and relatively short limbs (TL/S-V range = 0.34–0.46). All members of the complex exhibit exostosis

of the maxillary, premaxillary, nasal, frontoparietal and squamosal bones. On the dorsolateral body surfaces there are continuous or disrupted, longitudinally orientated skin folds commencing behind the skull, and terminating above the groin.

Nothing is known of the breeding biology of the members of the complex, but they are probably opportunistic breeders. The eggs are small and pigmented (ovidiameters of oviducal eggs range from 1.1 to 1.3 mm), and the tadpole (one species) is of the hylid type with two upper and three lower rows of labial teeth, an acuminate tail tip and a median or slightly dextral anus.

The geographic range of the complex extends from northern Western Australia to northern New South Wales (Fig. 1). Of what we demonstrate to be two component species, *C. australis* (*sensu stricto*) occurs in northern Western Australia, the Northern Territory and northern Queensland to the west of the Dividing Range; *C. novaehollandiae* is found throughout Queensland and extends as far south as the northern part of New South Wales.

Cyclorana australis (Gray).

FIG. 2A

Alytes australis Gray (1842).

Chiropletes australis, Gunther (1858); Boulenger (1882) (part).

Phacops australis, Fry (1914).

Cheiropletes australis, Spencer (1901) (replacement name for *Chiropletes*).

Cyclorana australis, Parker (1940) (part).

Type locality: "North coast of Australia". (Port Essington, Northern Territory.)

Material examined: Western Australia—WAM, R8732, Carlton Reach, Ord River; WAM, R43067, Crystal Ck; WAM, R1558-59, Drysdale River Mission; WAM, R21233, Fossil Downs; WAM, R1377, 43282-86, 42399-42422, Kalumburu; WAM, R22369-75, Kimberley Research Stn; SAM, R4769-70, R5070, Kununurra; WAM, R1654-57, Lander Sin; WAM, R42387, 80 km S of La Grange; WAM, R42536-40, R2381, 43478, 43491, Mitchell Plateau; WAM, R42530-35, Main Ord River Dam Site (spillway); WAM, R42424, Mt Hart; WAM, R32099, Mt Anderson; WAM, R32291, Mt Barnett; NR, 1562, Mowla Down; WAM, R13726, Oscar Ranges; NMV, D2354-55, Port George IV; WAM, R32149, St George Range; WAM, R11208, R11894, R12332, Wotjulum; WAM, R26769-70, Point Springs, Webber Range; WAM, R32351A, Wyndham; WAM, R25093, 40 km SE of Wyndham; WAM, R20307, Yeda Crossing, Northern Territory—SAM, R14332, Adelaide River; NMV, D12702, Harrow Ck; NMV, D8307, D8315, D8327, QM, J1785, 2985, SAM,



Fig. 1. Geographic distribution of the frogs of the *Cyclorana australis* complex. Circles = *C. australis*; triangles = *C. novaehollandiae*. Closed symbols indicate sites of the material examined, and the open circles one of the following literature references: Brattstrom (1970), Loveridge (1935), Moore (1961), Parker (1940), Stevin (1935).

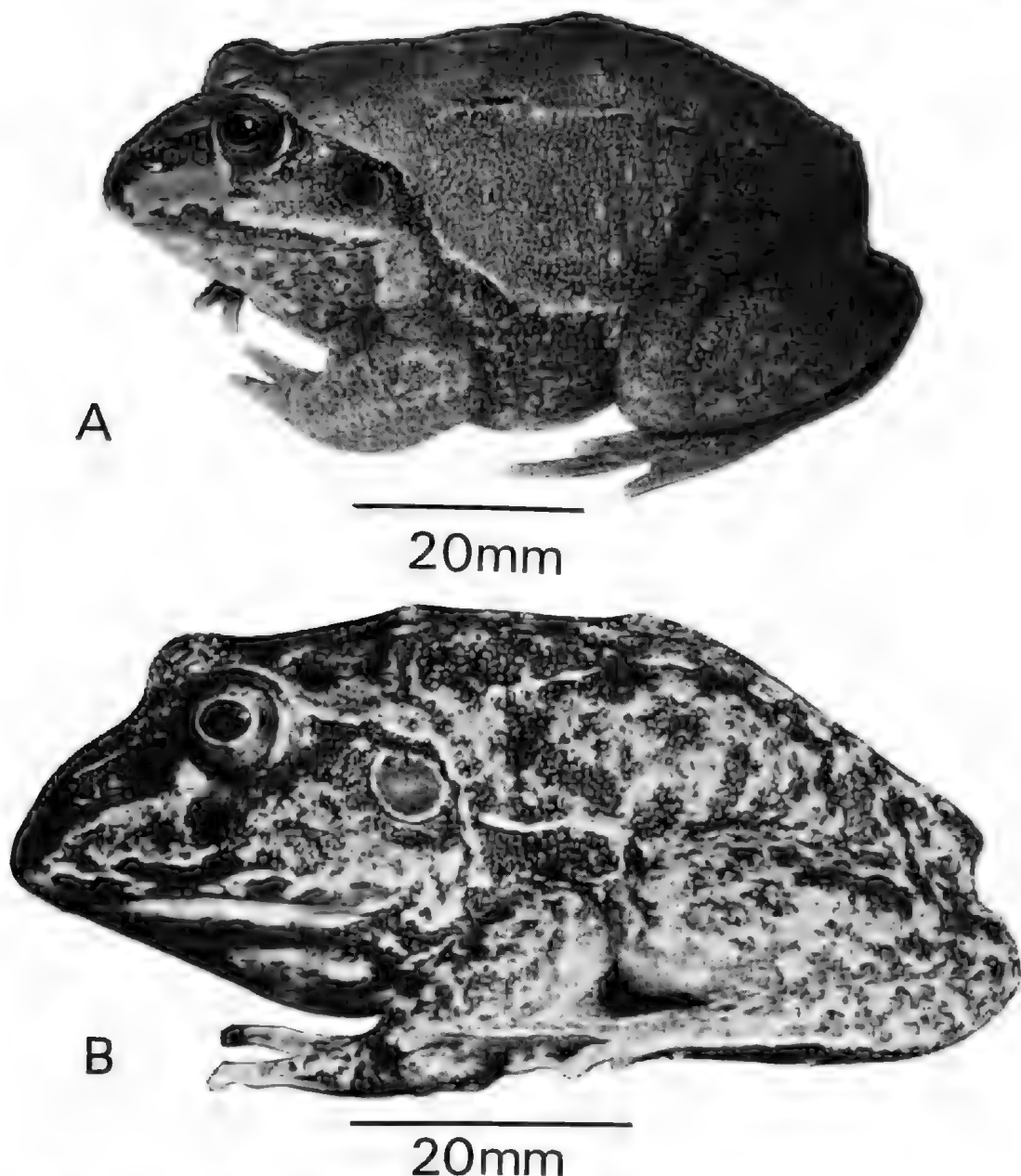


Fig. 2. A. *Cyclorana australis* from Kununurra, W.A. B. *Cyclorana novaehollandiae*, 15 km N of Goondiwindi, Qld.

R8968, Darwin; SAM, R13453, Elsey; SAM, R13450, Howard Springs; WAM, R1935-36, R21318, SAM, R14330-31, Katherine; SAM, R4877, Mt Bundy Stn; SAM, R13349 A-G, Smith Pt, Coburg Peninsula; WAM, R24007, Snake Ck; NMV, D12704-08, SAM, R13275 A-L, Tennant Creek; NTM, 498, 525-26, 50 km N of Tennant Creek. *Queensland*—SAM, R5010, R5070, Doomadgee Stn; NMV, D8437-38, SAM, R4934, Mornington I.

Description: The diagnostic characters of this species are: size large, males 70.8–78.0 mm and females 71.0–81.0 mm in snout to vent length; S-V/HW ratio high (mean 2.31); head width only slightly greater than head length (mean HL/HW ratio 0.89); TL/S-V ratio moderate (mean 0.32); foot relatively long (F/S-V mean 0.40).

Development and exostosis of the superficial skull bones are moderate in this species. The dorsal limit of the squamosal is such that there is a very broad gap between the squamosal and the frontoparietal. On the frontoparietal exostosis is confined to the lateral borders of the bone. The sub-orbital portion of the maxilla slopes steeply to the labial margin and is not expanded there into a lateral ridge.

Cyclorana australis is usually pale olive or grey in preservative and bears a narrow and very sharply demarcated dark brown rostral bar and a narrow sub-ocular bar which terminates far above the labial margin. The lateral body surfaces are commonly heavily suffused with darker pigment. The backs of the thighs are darker and densely variegated with light pigment.

Geographic variation: The presence of darker, irregular patches on the dorsum varies through the range. Dorsal spots are absent from a series of over 100 specimens from Kununurra. Specimens from Tennant Creek have light suffusions of pigment, and those from the north-eastern portion of the range are heavily pigmented with dark stippling. Immaculate and marked specimens occur on Mornington Island.

Variation in some of the pertinent body proportions is summarized in Table 1.

Eggs: A gravid female from Kununurra contained approximately 1000 eggs varying from 1.1 to 1.3 mm in diameter. The eggs have black animal poles.

Larval morphology: A series of tadpoles was obtained at Kununurra on the Ord River by K.

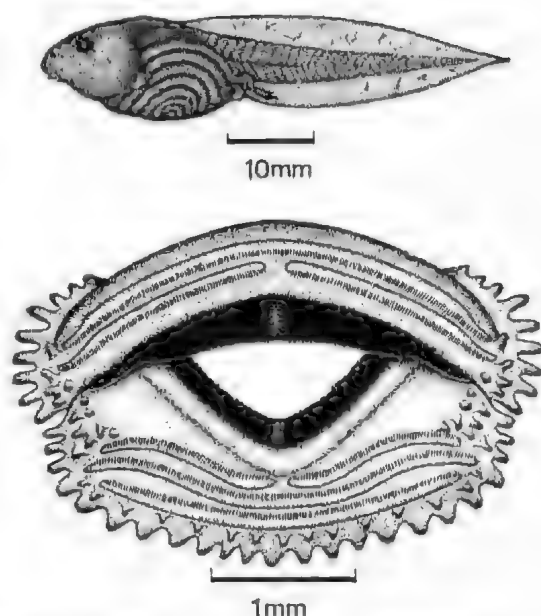


Fig. 3. Tadpole and tadpole mouthparts of *Cyclorana australis*.

Cole in February, 1963. The following notes are based on four specimens from this series at stages 36–39. All specimens are poorly preserved and badly distorted, so that their total length range of 50–65 mm is only an approximation.

The spiracle is sinistral and the anus median or very slightly displaced dextrally. The overall appearance (Fig. 3) is similar to that of *C. cultripes* and *C. platycephalus* (Watson & Martin 1973).

TABLE 1
Geographic variation in proportions of *Cyclorana* species
(Ranges are given with means and standard deviations in parentheses)

| Species and locality | n | HL/HW | TL/S-V | S-V/HW | F/TL | F/S-V |
|--------------------------|---|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|
| <i>C. australis</i> | | | | | | |
| Kununurra, W.A. | 7 | 0.81 — 0.93 (0.86 ± 0.04) | 0.38 — 0.45 (0.42 ± 0.03) | 2.13 — 2.33 (2.23 ± 0.09) | 0.91 — 1.00 (0.97 ± 0.03) | 0.38 — 0.44 (0.41 ± 0.02) |
| Smith Point, N.T. | 7 | 0.89 — 0.93 (0.91 ± 0.01) | 0.40 — 0.45 (0.43 ± 0.02) | 2.27 — 2.44 (2.36 ± 0.06) | 0.92 — 0.98 (0.95 ± 0.02) | 0.39 — 0.43 (0.41 ± 0.01) |
| Tennant Creek, N.T. | 7 | 0.87 — 0.94 (0.90 ± 0.02) | 0.40 — 0.46 (0.42 ± 0.02) | 2.25 — 2.49 (2.36 ± 0.08) | 0.91 — 0.98 (0.94 ± 0.02) | 0.38 — 0.42 (0.39 ± 0.01) |
| Mitchell Plateau, W.A. | 4 | 0.95 — 0.99 (0.97 ± 0.01) | 0.44 — 0.50 (0.46 ± 0.02) | 2.26 — 2.51 (2.41 ± 0.12) | 0.88 — 1.05 (0.95 ± 0.07) | 0.38 — 0.43 (0.41 ± 0.01) |
| <i>C. novaeollandiae</i> | | | | | | |
| Cooktown, Qld | 7 | 0.81 — 0.83 (0.83 ± 0.02) | 0.39 — 0.43 (0.41 ± 0.01) | 1.93 — 2.08 (2.02 ± 0.04) | 0.87 — 0.96 (0.91 ± 0.03) | 0.36 — 0.41 (0.38 ± 0.01) |
| Calliopi, Qld | 3 | 0.82 — 0.88 (0.86 ± 0.03) | 0.39 — 0.40 (0.39 ± 0.01) | 2.03 — 2.17 (2.12 ± 0.01) | 0.89 — 0.94 (0.92 ± 0.02) | 0.34 — 0.39 (0.36 ± 0.01) |
| Cunamulla, Qld | 5 | 0.78 — 0.85 (0.82 ± 0.03) | 0.34 — 0.41 (0.37 ± 0.02) | 1.97 — 2.13 (2.05 ± 0.06) | 0.93 — 1.02 (0.96 ± 0.03) | 0.32 — 0.39 (0.36 ± 0.03) |

The mouth is subterminal (Fig. 3) with a large horny beak and papillae around the sides and back of the mouth disc. There are two upper rows of labial teeth, the second disrupted medially, and three lower labial rows of which the first is similarly disrupted.

Mating Call: Calls of five individuals were recorded on 13.xii.1971, 14 km E of Daly Waters, N.T. The frogs were calling on land beside a small water-filled channel. Wet-bulb air temperature at the calling sites was 24.1°C. The call is a short, well-tuned note repeated in long sequences. The mean call duration is 152 msec (range 122–204). The fundamental frequency is 199 Hz (range 183–209), but contains little energy: most of the energy is in the third, fourth and fifth harmonics (about 600, 800 and 1,000 Hz) which are approximately equally emphasized.

Geographic Range: *Cyclorana australis* extends from the Kimberley District of northern Western Australia in the Gulf District of Queensland. In the Kimberleys it is clearly widely distributed, and in the Northern Territory it extends as far inland as Barrow Creek. Absence in the north-western portion of the Northern Territory may simply reflect inadequate sampling.

Cyclorana novaehollandiae Steindachner.

Cyclorana novaehollandiae Steindachner (1867).

Phractoptes uluataensis Peters (1867).

Chiroleptes australis, Boulenger (1882) (part).

Phractoptes australis, Loveridge (1935).

Cyclorana australis, Parker (1940) (part); Moore (1961), plate 35, Fig. 2.

Type locality: Rockhampton, Qld.

Material examined: Queensland—NMV, D13049, SAM, R9817, R9835, Battle Camp; MUZD, 90-92/70, 5 km SW of Calliope; QM, J431, Colesseum; QM, J18062, J18066, Condamine River, Cecil Plains; NMV, D13049, SAM, R11523-24, Cooktown; QM, J20685-91, 8 km W of Cooktown; SAM, R9690, Edward River Stn; QM, J2184-85, J12944, Eidsvold; QM, J14383-84, Gilruth Plains, Cunnamulla; MUZD, 56-58/70, 75/70, 9 & 15 km E of Goondiwindi; QM, J5611-12, Mackay; SAM, R4743, Mapoon Mission Stn; SAM, R9734, Mary River; QM, J14159-67, Mitchell R. Mission; SAM, R10419, Prestwood, Gilbert River; SAM, R3640, Rockhampton; QM, J10482, SAM, R3686, St George; QM, J2186-89, Stannary Hills; SAM, R1935, Stewart River; SAM, R9691, Strathgordon (N.S.); QM, J22227-29, Surat; NMV, D7542, QM, J4644, Townsville; QM, J3480, Victoria, Coongoola; QM, J18063-65, Waratah Stn, Cunnamulla.

Description: Snout to vent length of males 61.4–81.4 mm, females 74.8–101.2 mm; head noticeably broader than long (HL/HW mean 0.83); S-V/HL ratio low (mean 2.05).

TL/S-V ratio rather low (mean 0.40); foot short (F/S-V mean 0.37).

There is extreme exostosis of the skull bones. The squamosal in large specimens is usually so heavily overlain with secondary bone that it is visible through the skin, forming humps resembling parotoid glands, and extends so far superiorly that it approaches the margins of the frontoparietals. The frontoparietal is entirely exostosed, but the lateral margins are raised by bone deposition, so producing a deep, median furrow. The suborbital portion of the maxilla projects, forming a high and often concave shelf.

The constricted pupil in six living specimens from Cooktown approximated a rhomboid shape (see discussion).

In preservative, *C. novaehollandiae* is pale brown or grey, and is immaculate, lightly marked with scattered dark brown or blackish markings, or else very densely pigmented with such markings. The suborbital marking is broad and usually reaches the labial base of the maxilla. The backs of the thighs are usually very dark leaden grey and lack lighter vermiculations.

In life the series from Cooktown were an immaculate dull sandy yellow dorsally. The rostral stripe was dark brown, and similarly colored, small disrupted patches occurred on the inferior margin of the maxilla. The iris was golden and suffused with dark brown laterally and inferiorly. The posterior surfaces of the thighs were leaden grey, whilst the ventral surface of the body wall was a dull pearl bearing faint grey vermiculations on the throat.

Geographic variation: There is considerable variation in skull structure and coloration of the dorsum of this species. Comparison of small samples of extreme variants led us to conclude initially that two species were involved. Examination of larger series, however, has revealed the occurrence of forms of intermediate appearance. The variation may be summarized as follows. All specimens from central and southern Queensland have high skulls with a gently sloping maxilla and a densely pigmented dorsum. There is striking variation in individuals from northern Queensland. Some are densely pigmented whilst others are immaculate. The skull of the immaculate individuals is either similar to that of the pigmented frogs, or is spatulate and distinctly flattened. Unfortunately we have been unable to devise a means of objectively estimating skull depth with any degree of accuracy. We

hold the opinion that the high and the spatulate forms of the skull represent different evolutionary trends of development.

Whereas the extremes are clearly different, assessment of the significance of the observed variation is complicated by the existence in northern Queensland of a number of intermediate forms that cannot be referred to either form. In addition there are animals in which the terminal portion of the skull is more elongated. This variant occurs only on the Cape York Peninsula and at localities at the base of the Gulf of Carpentaria. Morphometric data of two small series are summarized in Table 1.

Eggs: Oviducal eggs of three gravid females ranged from 1.1 to 1.3 mm in diameter. An estimate of the number in one individual exceeded 1,000. The eggs have black animal poles.

Mating Call: The mating calls of two individuals recorded 5 km SW of Calliope, Queensland, on 18.i.1970, are very similar to those of *C. australis*. The frogs were calling on land beside a rain-filled roadside ditch, with a wet-bulb air temperature of 24.6°C. The spectral structure of the calls of the two species is essentially identical, with *C. novaehollandiae* also having emphasized harmonic bands at about 600, 800, and 1,000 Hz. However, its call duration is considerably longer (mean 249 msec: range 235–262 msec). Judged on the basis of the levels of difference in mating call structure of sympatric anuran species, this difference in duration does not represent divergence of sufficient magnitude to achieve reproductive isolation. Hence if *C. australis* and *C. novaehollandiae* occur in sympatry (as they may in the Gulf District) we would expect them to hybridize. A similar pattern of marked morphological differentiation, accompanied by very little mating call divergence, characterizes the Western Australian *Limnodynastes dorsalis* and the eastern *L. dumerili* (Martin 1972).

Geographic Range: *Cyclorana novaehollandiae* ranges from the Cape York Peninsula of northern Queensland to the New South Wales border.

KEY TO ADULTS

Back of thighs variegated, suborbital bar narrow and not reaching base of maxilla; maxilla gently sloping and not expanded laterally . . . *C. australis*

Back of thighs not variegated; suborbital bar (if present) usually broad and reaching base of maxilla; maxilla expanded to form lateral shelf

C. novaehollandiae

Discussion

The morphological complexity of *C. novaehollandiae* as defined here is unparalleled amongst Australian anurans. We believe that a study of species isolating mechanisms, such as male mating call, in north-eastern Australia could reveal the existence of two or possibly even three species. Our action of resurrecting *C. novaehollandiae* from the synonymy of *C. australis* is therefore only the first step towards an understanding of the *C. australis* complex. The biological data, e.g. mating call structure, that are necessary for final resolution of the problem may be extremely difficult to obtain. The northern Queensland populations are apparently opportunistic breeders which may call at a locality on only one or two nights each year (C. Tanner, pers. comm.). It seems justifiable, therefore, to treat the complex at this preliminary level.

In terms of skull structure, *C. australis* is clearly the most simplified and primitive member of the complex, exhibiting limited development of skull bones and the least extensive exostosis. All the variations in the form of the skull and exostosis of the cranial bones such as the maxillary and squamosal in *C. novaehollandiae* can reasonably be derived from *C. australis*.

The concept of *C. australis* being the primitive member may be acceptable morphologically, but it is more difficult to conceive zoogeographically in view of the absence of any member of the genus *Cyclorana* in New Guinea. The geographic area occupied by the members of the *C. australis* complex includes both high rainfall and relatively arid areas; i.e. it does not appear to be limited climatically. Thus if the complex originated in northern or north-western Australia it is surprising that it should be absent from New Guinea. Jennings (1972) estimates that the most recent land communication with New Guinea at Torres Strait terminated only 6,500–8,000 years ago; thus it is possible that colonization of north-eastern Australia by the complex occurred subsequently.

The gross differences in morphology characterizing the members of the *C. australis* complex represents a situation unique among Australian anurans. Differentiation in other species complexes, even those with extensive disjunctions of range (e.g. south-eastern and south-western Australia) is accompanied by only slight morphological divergence. It seems

probable, therefore, that the complex is of considerable antiquity. Two further circumstances lend support to this suggestion. One is the affinity of *Cyclorana* with the Hylidae demonstrated by Tyler (1972) and Watson & Martin (1973). The other stems from our observations on the pupil shape of *C. novae-hollandiae*. As stated above, the constricted pupil of *C. novae-hollandiae* is almost rhomboid. In fact, the ventral margin is an obtuse angle and the upper a broad curve. This curvature is difficult to detect during extreme constriction. Lynch (1971) considers the vertically orientated pupil to be the primitive and the horizontal pupil the derived state. However, from the fact that *Nyctimystes* (a genus that can only be derived from *Litoria*, a horizontally-pupilled stock) has a vertical pupil, it is clear that vertical orientation can be a derived state. The trend to one or other orientation of pupil shape could be accomplished

most readily from a rhomboid. That such a structure occurs in living *Cyclorana* is consistent with our hypothesis of its antiquity.

Acknowledgments

For the donation of specimens or the loan of those in their care we are indebted to Mr K. Cole, Miss J. Covacevich, Mr J. Coventry, Mr D. Howe, Dr B. S. Low, Dr G. Storr, Mr C. Tanner and Dr G. Vestergren. Mr G. F. Watson assisted in the field. Photographs were provided by Mr B. N. Douetil and the tape of the mating call of *C. australis* by Dr B. Low and Dr D. Gartside.

Our thanks are also due to Dr J. Ling for reading the manuscript, and to the Trustees of the Science and Industry Endowment Fund for providing travel funds to M.J.T. permitting visits to various Australian museums to examine collections.

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TRANSACTIONS OF THE
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THE IDENTITY AND STATUS OF THOMAS "LECTOTYPE" OF LEPORILLUS APICALIS (GOULD, 1853) [RODENTIA: MURIDAE]

BY J. A. MAHONEY*

Summary

MAHONEY, J. A. (1975) .-The identity and status of Thomas' "lectotype" of *Leporillus apicalis* (Gould, 1853) [Rodentia: Muridae]. *Trans. R. Soc. S. Aust.* 99(3), 101-104, 30 August 1975.

The specimen selected by Thomas as the lectotype of *Leporillus apicalis* (Gould, 1853) was misidentified by him and belongs to *Leporillus conditor* (Sturt, 1848). It does not belong to the type series of *L. apicalis*, therefore Thomas' lectotype selection for that species is invalid. The type material of *L. apicalis* and *L. conditor* is missing. Thomas' "lectotype" of *L. apicalis* and a second specimen of *L. conditor* in the British Museum (Natural History) could belong to the type series of *L. conditor*. Evidence for the occurrence of *L. apicalis* in Tasmania is lacking.

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Introduction

The name *Hapalotis apicalis* was proposed by Gould (1853a) for a new species of rodent from Australia. He did not state in the original description if one or more specimens were being described nor did he give any locality. Later, Gould (1853b) stated that he possessed a single example procured by Mr Strange in South Australia, and he illustrated the external features.

Thomas (1906a) nominated *Hapalotis apicalis* as the type species of a new genus, *Leporillus*, and subsequently (Thomas 1921a) he selected British Museum (Natural History) specimen 1853.10.22.15¹ as the lectotype of *Leporillus apicalis*, describing it as a female from S. Australia. Explaining his lectotype selection, Thomas (1921c) stated that although Gould had in his collection two specimens of that species, he seems to have done his describing from only one of them (BM, 53.10.22.14 (sic)—*lapsus* for BM, 53.10.22.15)

—the worst of the two, young, and with an imperfect tail. Thomas concluded with the remark that probably from memory, and certainly wrongly, Gould stated that the species had a white-tipped tail, but his overlooked second specimen [adult with nearly perfect skull² and quite perfect tail (BM, 53.10.22.14)] has the latter organ uniformly blackish or brownish above and dull white below, and there is no indication of the white tail-tip found in so many Australasian Muridae.

A study of three Australian Museum specimens of *L. apicalis*, and the literature, enabled Troughton (1923) to confirm that Gould was correct in attributing a white tail-tip to the species. Troughton stated also that Thomas' remark that Gould seems to have done his describing from only one of his two specimens means that that specimen must be accepted as the holotype.

Tate (1951) treated specimens 1853.10.22.14 and 1853.10.22.15 as "cotypes" of *L. apicalis*

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¹ The first two digits of British Museum (Natural History) registration numbers of mammals are frequently omitted from publications. Thus Thomas uses 53.10.22.15 for 1853.10.22.15.

² This skull is registered as 1854.10.21.1 and the Register entry mentions a stuffed specimen and refers to 53.10.22.16. I have been unable to find a specimen numbered 1853.10.22.16 in the British Museum (N.H.) therefore I am following Thomas' conclusion that 1853.10.22.14, 1853.10.22.16 and 1854.10.21.1 belong to the one individual; but it is possible that 1853.10.22.14, identified as *Hapalotis apicalis* in the Register, is lost and the skin now numbered 1853.10.22.14 is skin 1853.10.22.16 with an incorrect number. A note in Thomas' handwriting attached to skin 1853.10.22.14 and stating that this specimen was considered to be the type seems to refer to the Museum Register where "type" has been written opposite the number 1853.10.22.16. A portion of the posterior half of the cranium, and the left mandibular ramus, are missing from the skull.

TABLE 1

Skull measurements (in mm) of Thomas' "lectotype" of *Leporillus apicalis* (Gould), B.M. (N.H.), 1853.10.22.15.

| | |
|--|-----|
| Maximum width across nasals | 5.0 |
| Minimum width across right zygomatic plate | 4.4 |
| Length of right M ¹⁻³ | 9.7 |
| Width of left M ¹ | 2.6 |
| Width of left M ² | 2.7 |
| Width of left M ³ | 2.4 |
| Length of left M ₁₋₃ | 9.1 |
| Width of left M ₁ | 2.4 |
| Width of left M ₂ | 2.7 |
| Width of left M ₃ | 2.4 |

The teeth measurements are for the crowns of the teeth.

and referred to them as adult and young females, from "South Australia", collected by F. Strange. He briefly described the skin and skull of each and recorded measurements of them. He does not refer, in his account of *L. apicalis*, to Thomas' lectotype selection or to Troughton's recognition of a holotype for the species.

Identity of the "lectotype"

British Museum (N.H.) specimens 1853.10.22.14 and 1853.10.22.15 are examples of *Leporillus conditor* (Sturt, 1848) and not specimens of *Leporillus apicalis* (Gould, 1853) as believed by Thomas. They do not agree with the original description of *L. apicalis* (Gould) and because of this I do not accept that either of them belong to the type series of that species. Consequently, I regard as invalid Thomas' lectotype selection for *L. apicalis*. Thomas (1921b) stated there is no specimen of *L. conditor* in the British Museum, and further demonstrated his unfamiliarity with its characters by suggesting that it possibly belongs to *Notomys*, a genus of Australian hopping mice and rats.

Measurements of the badly damaged skull of Thomas' "lectotype" are given in Table 1. The skull is illustrated in Figs 1-4.

Discussion

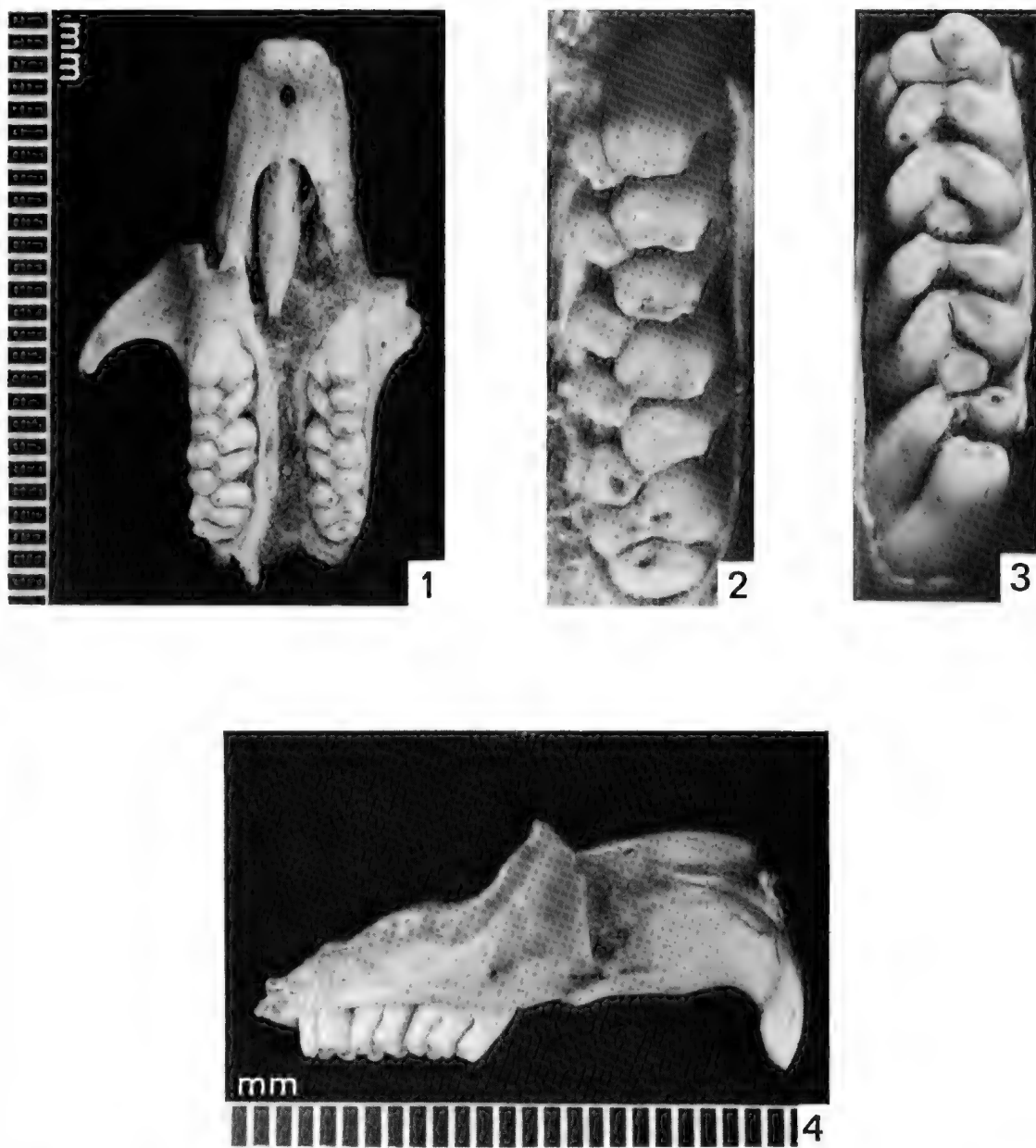
The type material of both *L. apicalis* and *L. conditor* is lost. The latter species was described by Sturt in 1848 as *Mus conditor* from specimens observed and collected on his

1844-6 Expedition to Central Australia. The original description was published in the Narrative of the Expedition and Sturt did not say where his material was deposited. It seems likely however that at least one specimen, illustrated by J. Gould and H. C. Richter in a plate³ accompanying Sturt's description of the species, would have gone into Gould's collection, and perhaps from there into a Museum collection. A collection of mammals made by the Expedition was presented to the British Museum by Sturt in 1846. This collection is noted by Thomas (1906b) and does not contain specimens of *Leporillus*.

Specimens 1853.10.22.14 and 1853.10.22.15 were registered in the British Museum on October 22nd, 1853, and were acquired from Gould. Labels attached to them refer to S. Australia and F. Strange. The entries for them in the Register mention neither a locality nor Strange. S. Australia could be an abbreviation of either South Australia or Southern Australia and F. Strange presumably is Frederick Strange, a collector and dealer in natural history specimens who accompanied Sturt on some of his early surveys (but not the 1844-6 Expedition), and was an early settler in South Australia and later, in the 1840's, a resident of New South Wales (Whitell 1947). Gould (1849) does not mention Strange and South Australia in his account of *L. conditor*. Subsequently (Gould 1863) he gives only the interior of New South Wales and Victoria as localities for the species. It is possible that the inscriptions on the labels are interpretations of the origins of the two specimens based on Gould's account of *L. apicalis*. If they are not interpretations, their significance is uncertain since the citation of S. Australia is ambiguous and Strange might not be the collector of the specimens.

British Museum (N.H.) specimens 1853.10.22.14 and 1853.10.22.15 could have been collected on Sturt's 1844-6 Expedition and might belong to the type series of *L. conditor*. This is so even if they came from South Australia. Sturt (1848, Vol. 1, pp. 120-121) referred in his account of the Expedition's progress along the Darling River in New South Wales to an individual of *L. conditor* secured by Mr Browne and to one, a male, obtained by himself from a native. However, Sturt (Vol. 2, Appendix, p. 4) noted also that the last nest

³ Gould's name is printed on this plate and the species name *Mus conditor* is attributed to him by Sturt; nevertheless Sturt is the author of the name *Mus conditor*.



Figs 1-4. *Leporillus conditor* (Sturt, 1848). British Museum (N.H.) 1853.10.22.15. Thomas' "lecto-type" of *Leporillus apicalis* (Gould, 1853). Fig. 1—Ventral view of cranium (x3). Fig. 2—Occlusal view of left upper molar row (x8). Fig. 3—Occlusal view of left lower molar row (x8). Fig. 4—Right lateral view of cranium (x3).

of *L. conditor* was found on the bank of the muddy lagoon to the north of the Pine Forest (N.S.W.), and the Expedition explored portion of South Australia before reaching the muddy lagoon.

Although the whereabouts of the type material of *L. apicalis* and *L. conditor* is un-

known, there is no uncertainty about which species of native rodents were named *Hapalotis apicalis* and *Mus conditor* by Gould and Sturt respectively, and neotype selections for them are unwarranted.

Gould (1853b) commented in his account of *L. apicalis* that an animal in spirits in the

British Museum, presented by R. C. Gunn, from Van Diemen's Land, accords very closely with it in the colouring of the fur and in the rat-like form of the tail. He added that it is of much smaller size than *L. apicalis* and in all probability will prove to be a new species. Gould's listing in 1863 of Van Diemen's Land as a possible locality for *L. apicalis* could be based on that material. Tasmanian rodent specimens in the British Museum (N.H.) and attributable to Gunn are recorded in the Register. The identities of these specimens and their registration numbers are *Rattus rattus* (Linnaeus, 1758) (1837.6.10.56), *Rattus norvegicus* (Berkenhout, 1769) (1838.1.15.17),

Rattus lutreolus (Gray, 1841) (1845.5.2.3, 1852.1.15.16, 1852.1.15.17), *Mastacomys fuscus* Thomas, 1882 (1852.1.15.15) and *Pseudomys higginsi* (Trouessart, 1897) (1852.1.15.18). None of these are *L. apicalis*, and evidence for the occurrence of this species in Tasmania is lacking.

Acknowledgments

This study was carried out in the British Museum (N.H.) by arrangement with Dr G. B. Corbet of the Mammal Section. The photographs were taken by Mr F. Greenaway, British Museum (N.H.) Photographic Unit.

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REVISION OF THE GENUS *ASTRAEUS* LAPORTE & GORY (COLEOPTERA: BUPRESTIDAE)

BY S. BARKER*

Summary

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Introduction

There are 27 described species of the genus *Astraeus* from Australia and one from New Caledonia. Originally established as *Asthraeus* by LaPorte & Gory (1837), the genus was referred to by that name until Gemminger & de Harold (1869) used *Astraeus*, thus correcting an incorrect transliteration from the Greek. This has been followed by all subsequent authors. Barker (1964) requested the International Commission for Zoological Nomenclature to validate the emendation of *Asthraeus* to *Astraeus* and this was eventually carried out (I.C.Z.N. 1966, Opinion 795). The genus was last revised by van de Poll (1889) who gave excellent descriptions and illustrations of all species known at that time. Presumably van de Poll never saw a live specimen of the genus, so would have been unaware of their unique spring mechanism involving the release of the elytra from the closed position. When the living beetle releases the spring, the elytra flick open with such force that the insect can be projected for up to several metres. The effect is reminiscent of the sternal spring of the Elateridae except that the

same result is achieved in a different way. It has no doubt evolved as an escape mechanism. One other feature has apparently not been commented on in the literature and that is the fact that most of the species exhibit classical warning colouration of yellow markings on a dark background. Whether any of the species are noxious to predators or whether they are Batesian mimics has yet to be determined.

Since van de Poll's excellent monograph, further species have been described and more discovered so that the genus is again in need of revision. This poses some difficulty to an Australian worker as most of the type specimens are housed in overseas museums. Also, through habitat destruction throughout Australia, some of the species are not abundant over their former range and unfortunately the genus is very poorly represented in museums and in most private collections in this country. The adults of more than half of the species occur on *Casuarina* sp., but some are also associated with species of *Jacksonia*, *Banksia*, *Xanthorrhoea*, *Callitris*, *Melaleuca*, *Acacia*, *Daviesia*, and possibly *Dryandra* and *Hakea*. Adults of the early emerging species can be

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collected in August and adults of some species are present as late as March. More than half of the known species are found in the southern half of Western Australia. The others occur over the rest of the continent excluding the desert and northern-most tropical areas. One species occurs on New Caledonia. The genus is unknown from Tasmania.

In this paper male genitalia have not been used to diagnose the species, but have been used as one character to place the species into related groups.

This revision is based mainly on collections made by the author in New South Wales, South Australia and Western Australia between 1962-1975, now housed in the South Australian Museum. The remaining specimens are scattered throughout the collections listed below. The abbreviations used in the text for museum and private collections are as follows:

| | |
|------|--|
| EA | Collection of Mr E. E. Adams, Edungalba, Queensland. |
| AM | The Australian Museum, Sydney |
| ANIC | The Australian National Insect Collection, C.S.I.R.O., Canberra. |
| BPBM | The Bernice P. Bishop Museum, Honolulu. |
| BM | The British Museum (Natural History), London. |
| KC | Collection of Mr and Mrs K. Carnaby, Wilga, Western Australia. |
| JH | Collection of Mrs J. Harslett, Amiens, Queensland. |
| MM | The MacLeay Museum, Sydney (types on permanent loan to ANIC). |
| MNHN | Museum National d'Histoire Naturelle, Paris. |
| NM | The National Museum of Victoria, Melbourne. |
| NMP | National Museum, Prague. |
| QM | The Queensland Museum, Brisbane. |
| SAM | The South Australian Museum, Adelaide. |
| WADA | The Western Australian Department of Agriculture, South Perth. |
| WAM | The Western Australian Museum, Perth. |

The Australian Buprestidae have been divided into six sub-families (Britton 1970). *Astraeus* belongs in the sub-family Buprestinae, the members of which have mouthparts not produced downwards to form a rostrum. In the sub-tribe Buprestes the metathoracic epimera are completely exposed whereas in the Anthaxiae they are totally or partially covered by the lateral extension of the abdo-

men. *Astraeus* is placed in the sub-tribe Buprestes with nine other genera found in Australia. *Astraeus* and *Neobuprestis* both have an indistinct scutellum, but *Neobuprestis* has an exposed pygidium whereas in *Astraeus* it is covered by the elytra. All of the other Australian members of the sub-tribe have a distinct scutellum. They are: *Nascioides*, *Nascio*, *Neobubastes*, *Notobubastes*, *Bubastes*, *Buprestina*, *Buprestodes* and *Euryspilus* (Carter 1929).

Taxonomy

Genus *ASTRAEUS* LaPorte & Gory

Astraeus LaPorte & Gory, 1837: 1, pl. 1, fig. 1. (Invalidated, Opinion 795.) Imhoff, 1856: 46. Lacordaire, 1857: 43. Saunders, 1868: 10, pl. 1, fig. 12.

Astraeus: Gemminger & de Harold, 1869, 5: 1380. Saunders, 1871: 43. Masters, 1871: 124. MacLeay, 1873: 239-240. Kerremans, 1885: 136, van de Poll, 1886: 176-178. Masters, 1886: 71; van de Poll, 1889: 79-110, pls 2, 3, figs 1-19. Blackburn, 1890: 1256-1258; 1891: 496, van de Poll, 1892: 67-68. Kerremans, 1892: 101-102. Blackburn, 1892: 211-213; 1894: 101; 1895: 45-46. Kerremans, 1900: 295-296; 1902: 148-149. Falvel, 1904: 116. Carter, 1925: 229, fig. 1. Obenberger, 1928: 204-205. Carter, 1929: 265, 282, 302, pl. 33, fig. 43. Obenberger, 1930: 265-367. Carter, 1933: 41. Obenberger, 1936: 133. Barker, 1964: 306-307. I.C.Z.N., 1966: 269-270.

Astraeus: Carter, 1929: 270.

Type species, *Astraeus flavopictus* LaPorte & Gory, 1837 (by monotypy).

Generic description

Head. Medium size or large; the surface pitted; with a median longitudinal impressed line on the basal half; clypeus short; the apical margin with a bow-shaped indentation; labrum incised; antennal cavities small and rounded, situated near the lower internal corner of the eyes.

Antennae. The first segment longer than any of the rest, rounder and thicker at the apex than at the base; 2nd segment short and obconic; 3rd segment longer than the 2nd but not as long as the first, also obconic; 4th segment slightly shorter than the 3rd, dorsoventrally flattened, the front edge projecting outwards to form a tooth; the remaining segments, except the last, similar in structure to the 4th and each slightly smaller than the succeeding segment; the last segment flattened but not

toothed. In species belonging to *Astraeus* (*sensu stricto*) the antennae are sexually dimorphic, being longer in males than in females, due to the segments after the 3rd being of approximately equal length, whereas in females they become progressively shorter. In *Astraeus* (*Depollus*) the antennae do not show sexual dimorphism and are short in both sexes.

Pronotum. Surface pitted; wider than long; dorsally convex; rounded at the sides and narrower at the apex than at the base; a deep notch occurs on either side of the middle, at the base. In all but one species a small spindle-shaped depression is present at the base of the median lobe. I have called this structure the basal crypt (Fig. 24).

Scutellum. Invisible.

Elytra. Convex dorsally, each side with a crescent-shaped lobe fitting over the notches in the base of the pronotum; the apex of each elytron ends (with rare exceptions) in a sharp point, the sutural spine, usually formed by a crescent-shaped lateral emargination which forms on the inner edge a smaller lateral tooth, usually called the marginal spine; if the lateral emargination is absent, so is the marginal spine; below the shoulder the external margin is dilated, sometimes the dilation is rounded posteriorly, sometimes strongly projected backwards and angled forming a point, the whole being folded inwards and covering part of the metasternal coxae—this structure is called the humeral fold (Fig. 1); punctate-striate and in many cases also costate; there is a curved lip on the anterior undersurface of each elytron which fits over an opposite curved projection on the mesothorax, together forming the catch of a spring escape mechanism.

Undersurface. Variably pitted; anterior edge of prosternum straight or crescent-shaped and a large prosternal process; mesosternum short; metasternum approximately equal in length to the prosternum; posterior margins of coxae and abdominal sternites glabrous.

Legs. Femur slightly dorsoventrally flattened but robust; tibia almost cylindrical but longer than the femur; 1st tarsal segment longer than the remaining segments which become progressively shorter.

Body outline. Laterally teardrop-shaped, the apex being constricted; dorsally convex; ventrally straight at the anterior end and curving upwards at the end of the abdomen, rarely concave.

Key to the sub-genera of *Astraeus*

1. Lateral lobes of pronotum projecting from the elytral edge line; elytra striate-punctate but never with longitudinal costae; humeral fold rounded *Astraeus* (*Depollus*)
1. Lateral lobes of pronotum confluent with the elytral edge line; elytra striate-punctate with well or poorly developed longitudinal costae; humeral fold angled (Fig. 1) *Astraeus* (*sensu stricto*)

Sub-genus *Depollus* sub-gen. nov.

Type species *Astraeus aberrans* van de Poll, 1886.

Head medium sized. Antennae short. Pronotum notched on both sides at the base, with a median lobe pointed and projecting, the lateral lobes with the posterior margin curved upwards and outwards. Elytra striate-punctate, the edges of the striae never costate. The suture ends posteriorly in a short or very short spine which may be blunt or pointed and curved outwards. With no marginal spine or in one species with a very short, blunt marginal spine. The humeral fold is rounded and poorly developed. Only known to occur in Western Australia.

Key to the species of *Astraeus* (*Depollus*)

1. Basal colour brown 1. *polli* sp. nov.
1. Basal colour black 2
2. Elytra with 4 longitudinal red vittae 5. *lineatus* van de Poll
2. Elytra without longitudinal red vittae 3
3. Head, pronotum and undersurface very hairy 4
3. Head, pronotum and undersurface not very hairy 5
4. Pronotum with clumps of hair emerging from depressions towards the sides; no marginal spine 3. *robustus* sp. nov.
4. Pronotum with hair emerging singly, not clumped; small marginal spine 4. *aberrans* van de Poll
5. Head and pronotum with deep punctures closely packed together 2. *tanniensis* sp. nov.
5. Head and pronotum with shallow, separated punctures 6
6. Pronotum laterally inflated, elytral pattern numerous strigiform spots 6. *multinotatus* van de Poll
6. Pronotum not laterally inflated, elytral pattern small and large spots and longitudinal vittae 7
7. Sutural spine well developed and outcurving 7. *irregularis* van de Poll
7. Sutural spine poorly developed and not outcurving 8. *dedariensis* sp. nov.

1. *Astraeus* (*Depollus*) *polli* sp. nov.

FIGS 2, 22A

Types

Holotype: ♂, Wongan Hills, W. Aust., on *Casuarina campestris*, 9.1.1971, S. Barker, SAM. I 20940.

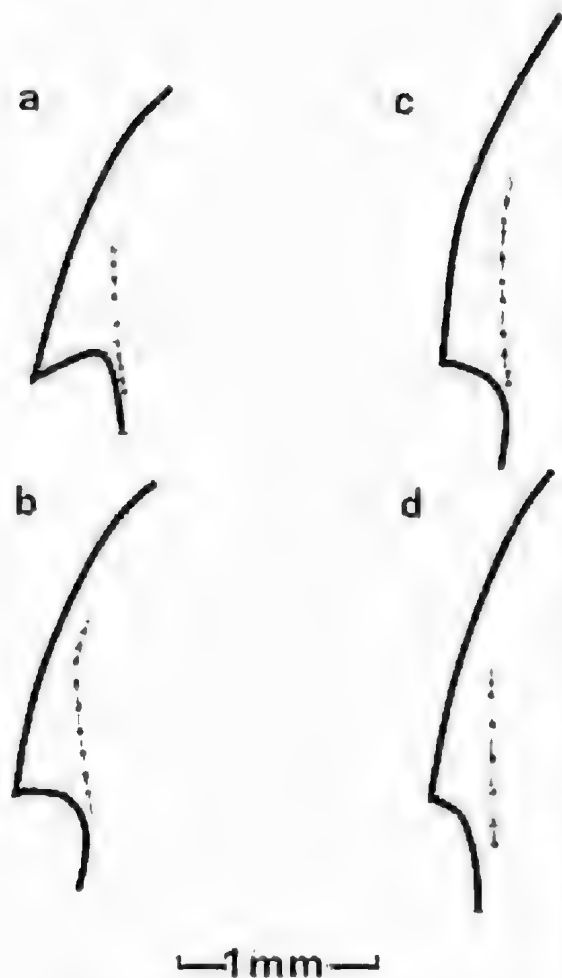


Fig. 1. Outline diagram of the left humeral fold of 4 species of *Astraeus*. The head end of each is to the top of the page and the left side is uppermost. Note that the specimens figured are all females and that (a) and (b) were smaller specimens than (c) and (d). Each structure is categorised as in the text. (a) *A. mustersi* MacLeay — well developed, acutely angled. (b) *A. samouelli* Saunders — well developed, angled. (c) *A. intricatus* Carter — moderately developed, angled. (d) *A. carnabyi* sp. nov. — poorly developed, slightly angled

Allotype: ♀, Wongan Hills, W. Aust. on *C. campestris*, 9.i.1971, S. Barker, SAM. 1 20941.

Paratypes: 1 ♂ & 1 ♀, 2 km W of Wongan Hills, W. Aust. on *C. campestris*, 20.i.1973, S. Barker, EA; 5 ♂ & 4 ♀, Wongan Hills, W. Aust. on *C. campestris*, 9.i.1971, S. Barker, ANIC (1 ♂ & 1 ♀), BM (1 ♂ & 1 ♀), MNHN (1 ♂ & 1 ♀), SAM (2 ♂ & 1 ♀); 1 ♂, Dedari,

W. Aust., 12.i.1948, J. A. Douglas, NM; 1 ♂, Dedari, W. Aust., WADA; 2 ♂, South Tamin Flora Reserve, W. Aust. on *C. campestris*, 6.i.1971 & 9.i.1971, S. Barker, WAM.

Colour. Shiny. Head brown with the following yellow markings: two lunettes from the inner corner of the eye, concave towards the base of the antennae but not reaching the middle of the head; behind each of the former at the base is a single small spot; a small spot at the base behind each eye; an elongate band runs from the anterior underside of the eye almost to the base; there is a large spot on each side of the gular; antennae brown. Pronotum brown with blue reflections and the following yellow markings: close to the anterior margin on each side of the centre, but not reaching it, is a laterally elongate mark; in the same line, directly behind the eye, is a smaller laterally elongate spot; towards the base, in the middle of each side, there is a longitudinally elongate spot, and between them a small median longitudinally elongate spot; laterally there is a longitudinally elongate spot commencing just after the middle, running to the base, which is flared outwards with a dark rim and the exposed inner surface is yellow. Elytra brown with blue reflections: the intervals between the striae are irregularly mottled with yellow, more so at the base than at the apex; the sutures, apical spines, and the lateral and anterior margins of the elytra are black but elsewhere brown. Undersurface brown: the mesosternum and metasternum each have lateral yellow patches and each of the abdominal segments have lateral yellow spots; the coxal plates each have a yellow spot near the centre but not touching it; hairs silver. Legs: femur and tibia, brown with blue reflections; tarsi dark brown with blue reflections.

Shape and sculpture. Head with shallow punctures, except for a median longitudinal glabrous line commencing between the eyes and confluent with the basal impressed line; with short sparse hairs. Pronotum with shallow punctures in the middle becoming confluent at the sides, except for two small round glabrous areas in the centre of each half; a short impressed line projecting forwards from the basal crypt; sides rounded and narrowed from base to apex. Elytra with the intervals between the striae slightly convex and transversely strigose with shallow punctures; parallel-sided until after the middle then rounded to the base; with a small sutural spine projecting laterally. Undersurface with shallow punctures,

denser at the sides than in the middle; with a few short hairs.

Size. Males $10.5 \pm 0.15 \times 3.8 \pm 0.07$ mm (18). Females $11.5 \pm 0.27 \times 4.0 \pm 0.09$ mm (18).

Distribution. Western Australia.

General remarks. Named after the late J. R. H. Neervort van de Poll.

Specimens examined. W. Aust.: Types; 5 ♂ & 3 ♀, 13 km N of Guomalling, on *Casuarina campestris*, 9.i.1971, S. Barker; 1 ♂ & 1 ♀, Waddington, on *C. campestris*, 9.i.1971, S. Barker; 1 ♂ & 2 ♀, Dedari, on *C. campestris*, 20.xii.1972, S. Barker; 3 ♂ & 3 ♀, 2 km W of Wongan Hills, on *C. campestris*, 20.i.1973, S. Barker.

2. *Astraeus (Depollus) tamminensis* sp. nov.

FIGS 3, 22B

Type.

Holotype: ♂, South Tammin Flora Reserve, W. Aust. on *Casuarina campestris*, 6.i.1971, S. Barker, SAM, I 20438.

Colour. Head and pronotum dull, elytra shiny. Head black, bottoms of most of the punctures yellow with the following yellow markings: two small elongate spots each between the eye and above the base of the antennae; laterally a small round spot between the eye and the base of the head; ventrally all yellow, almost continuous under the eye with the first mentioned spot; antennae dark brown with blue reflections. Pronotum black, bottoms of most of the punctures yellow, with the following yellow markings: a thin median longitudinal line from base to apex covering all but the tip of the median lobe; two longitudinal stripes on each side of the first, curving inwards from the base but ending before the apex, each capped with a circular spot near the apex; a thicker lateral stripe runs from the base to the apex; underside with alternate irregular stripes of black and yellow, the yellow predominating. Elytra with alternate black and yellow longitudinal stripes broken irregularly, their breadth conforming to the intervals between the striae; predominantly black along the suture and the outer margin, yellow in the middle. Undersurface mainly yellow with irregular black markings along the middle of each side across the outer margins of the abdominal sclerites and at the apex, the black markings all with brassy metallic gleams; hairs silver. Legs dark brown with blue reflections; each femur with elongate yellow markings on both surfaces.

Shape and sculpture. Head with dense, uniformly deep punctures. Pronotum with uniformly dense punctures; more or less parallel-

sided but abruptly rounded at the apex. Elytra with the intervals between the striae transversely wrinkled, and deeply and densely punctured; parallel-sided from base to behind the middle then uniformly rounded in the area where marginal spines occur in the other sub-genus, then straight sided to the apical spine which is minute. Undersurface closely and evenly punctured; with a few short hairs.

Size. Male 11.3×4.1 mm (1).

Distribution. Western Australia.

General remarks. This species shows closest affinity with *Astraeus polli*.

Specimens examined. Type only.

3. *Astraeus (Depollus) robustus* sp. nov.

FIGS 21, 22C

Types.

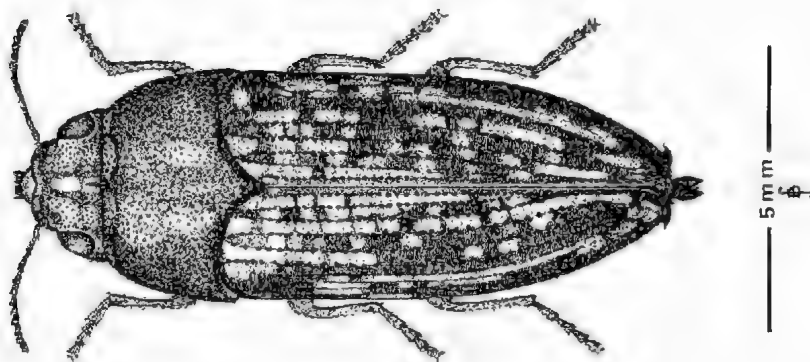
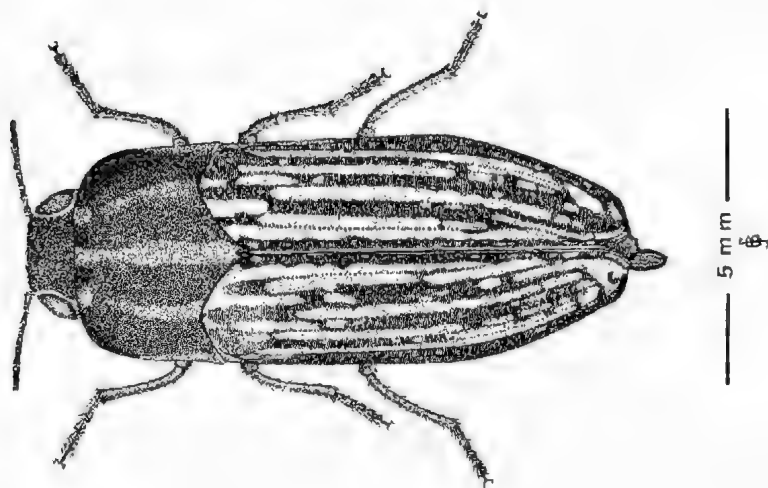
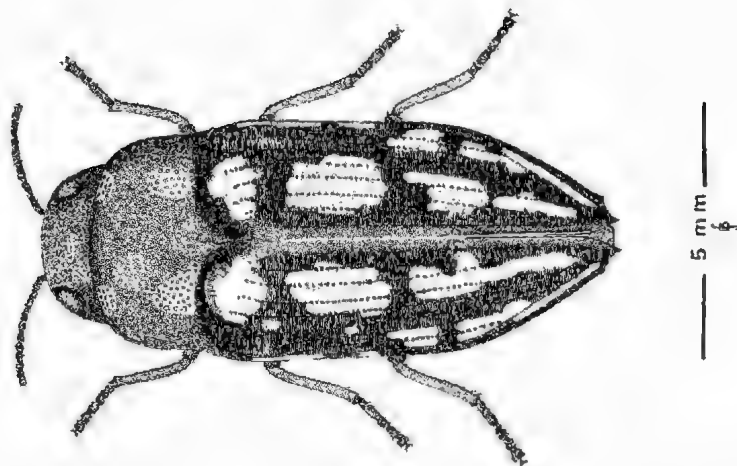
Holotype: ♂, Payne's Find, W. Aust., on *Casuarina dielsiana*, 17.ix.1970, S. Barker, SAM, I 20942.

Allotype: ♀, Payne's Find, W. Aust., on *C. dielsiana*, 17.ix.1970, S. Barker, SAM, I 20943.

Paratypes: 1 ♂, Payne's Find, W. Aust., on *C. dielsiana*, 17.ix.1970, S. Barker, ANIC; 1 ♀, Payne's Find, W. Aust., on *C. dielsiana*, 17.ix.1970, S. Barker, BM; 1 ♂ & 1 ♀, 383 km along Payne's Find Rd, W. Aust. on *C. dielsiana*, 17.ix.1970, S. Barker, MNHN; 1 ♂, Payne's Find, W. Aust. on *C. dielsiana*, 17.ix.1970, S. Barker, WAM.

Colour. Shiny. Head, pronotum and elytra black with purple reflections. Antennae black with blue and purple reflections. Elytra with the following yellow markings: a longitudinal spot in the 2nd outermost interstice near the shoulder and another just before the middle; a similar but larger spot lies on the 5th outermost interstice after the middle but not reaching the apex; a large round spot before the middle with the width of the 3rd-6th interstice from the suture; a variable number of small spots at the base of the elytra in the middle, the maximum number is four per side but they are absent in some specimens. Undersurface black with purple reflections; hairs silver. Legs brown: the joint between the femur and tibia black on the upper surface; 1st tarsal segment brown at the base and black at the apex as are the remainder.

Shape and sculpture. Head with dense shallow punctures; with a glabrous longitudinal median line between the eyes confluent with the basal impressed line; bairy. Pronotum sparsely and shallowly punctured in the middle where the depressions are small but greatly increase in size laterally where the non-depressed areas

Fig. 2. *Astraeus polli* sp. nov.Fig. 3. *Astraeus tumminensis* sp. nov.Fig. 4. *Astraeus dedariensis* sp. nov.

are glabrous; sides gradually rounded from base to apex; hairy, with hairs emerging singly in the middle and in clumps from the lateral depressions. Elytra with intervals between the striae slightly convex; more or less parallel-sided from base to just after the middle, then rounded gradually to the apex; with sharp sutural spines; hairy. Undersurface covered with punctures, shallow in the middle, deeper and denser at the sides; hairy, the hairs on the prosternal process and prosternum noticeably longer than elsewhere.

Size. Males $15.9 \pm 0.31 \times 5.6 \pm 0.16$ mm (4). Females $17.0 \pm 0.90 \times 6.0 \pm 0.25$ mm (3).

Distribution. Western Australia.

Specimens examined. Types only.

4. *Astraeus (Depollus) aberrans* van de Poll, 1886: 176; 1889: 84, 90, 91, pl. 2, fig. 4, 4a. Kerremans, 1892: 101; 1902: 148. Carter, 1929: 282. Obenberger, 1930: 365.

Astraeus aberrans var. *picicollis* van de Poll, 1889: 91. Kerremans, 1892: 101; 1902: 148. Carter, 1929: 282. Obenberger, 1930: 365.

FIG. 22D

Type. MNHN (not seen by author).

Colour. Shiny. Head, pronotum and elytra black with purple reflections; antennae black with blue and purple reflections. Elytra with the following yellow markings: a small irregular number of elongate markings each being restricted to the width of one interval between striae and occurring mainly in three areas: near the suture; in the middle of the elytra; next to the anterior part of the outer margin. Undersurface metallic purple, the lateral margin of the 1st, 2nd and 3rd abdominal segments each with a yellow spot which is variable in size and absent from the 3rd segment in some specimens; hairs silver. Legs dark with blue and purple reflections.

Shape and sculpture. Head deeply punctured, in parts in the middle less so than at the sides, the areas involved glabrous; with a longitudinal glabrous line between the eyes merging with the basal impressed line; very hairy. Pronotum with large deep punctures dispersed but more so in the middle with the elevated parts glabrous; mostly parallel-sided but abruptly rounded and narrowed at the apex; anterior margin projecting forwards in the middle; very hairy at the sides, the hairs emerging singly, not in clumps. Elytra with the intervals between the striae convex and slightly wrinkled, each with two longitudinal rows of small hairs; parallel-sided, rounded after the

middle to the small marginal spine; sutural spine small. Undersurface evenly and shallowly punctured; hairy.

Size. Males $14.0 \pm 0.2 \times 4.9 \pm 0.09$ mm (25). Females $16.6 \pm 0.43 \times 5.8 \pm 0.17$ mm (11).

Distribution. Western Australia.

General remarks. This species shows closest affinity with *Astraeus robustus*.

Specimens examined. W. Aust.: 1 ♂, Carnamah, 30.ix.1965, E. Baker; 12 ♂ & 6 ♀, 5 km W of Payne's Find on *Casuarina* sp., 17.ix.1970, S. Barker; 2 ♂, 106 km S of Payne's Find on *Casuarina corniculata*, 18.ix.1970, S. Barker; 2 ♀, Wialki on *C. corniculata*, 19.ix.1970, S. Barker; 1 ♂, Wialki on *Casuarina campestris*, 21.ix.1970, S. Barker; 1 ♂, South Tammin Flora Reserve on *C. campestris*, 30.ix.1970, S. Barker; 3 ♂ & 4 ♀, South Tammin Flora Reserve on *C. campestris*, 8.xi.1970, S. Barker; 3 ♂ & 1 ♀, Quaitading on *C. campestris*, 7.xi.1970, S. Barker.

5. *Astraeus (Depollus) lineatus* van de Poll, 1889: 84, 87-89, pl. 2, figs 2, 2a. Kerremans, 1892: 102; 1902: 149. Carter, 1929: 282. Obenberger, 1930: 366.

FIG. 22E

Type. Holotype, MNHN (not seen by the author).

Colour. Head and pronotum dull, elytra shiny. Head black with bronze-green reflections in the middle at the base, the rest with purple reflections; with or without a red spot underneath each eye; antennae black with purple reflections. Pronotum black with bronze-green reflections in the middle, the rest with purple reflections; a thin lateral red stripe on each side; with or without a small red spot on each side of the median lobe near the base. Elytra black with blue reflections and the following red markings: two broad vittae, the first near the margin, but not touching it, running from the shoulder to the preapical area; the second in the middle commencing near the front edge running parallel to the suture, but not touching it, to the preapical area. Each of the vittae may be entire or broken into two or a number of elongate marks. Undersurface metallic purple with lateral red marks on the prosternum, 3rd coxal plate and 1st, 2nd and 3rd abdominal segments. The presternal and 3rd abdominal spots are absent from some specimens; hairs silver. Legs: femur and tibia metallic purple; tarsi brown.

Shape and sculpture. Head evenly punctured with a longitudinal glabrous line between the eyes; hairy. Pronotum evenly punctured, the punctures deeper at the sides than in the

middle; sides narrowed and slightly rounded from the base to near the apex where they are more noticeably rounded; the front edge projecting forwards in the middle; hairs longer and more dense at the sides than in the middle. Elytra with the intervals between the striae convex with shallow punctures and faintly transversely strigose; laterally slightly concave from the shoulders until after the middle, then rounded to the small sutural spine; hairy. Undersurface: prosternum with large punctures, the rest with small shallow punctures, less dense in the middle; hairy.

Sizes. Males $11.0 \pm 0.48 \times 3.8 \pm 0.22$ mm (3). Females $13.0 \pm 0.29 \times 4.6 \pm 0.11$ mm (6).

Distribution. Western Australia.

Specimens examined. W. Aust.: 1 ♂, 5 km W of Payne's Find on *Casuarina* sp., 17.ix.1970, S. Barker; 1 ♂, South Tammin Flora Reserve on *Casuarina campestris*, 30.ix.1970, S. Barker; 2 ♀, Quairading on *C. campestris*, 7.xi.1970, S. Barker; 1 ♂ & 2 ♀, South Tammin Flora Reserve on *C. campestris*, 8.xi.1970, S. Barker; 2 ♀, 13 km N of Goomalling on *C. campestris*, 9.x.1971, S. Barker.

6. *Astraeus (Depollus) multinotatus* van de Poll, 1889: 84, 89, 90, pl. 2, fig. 3, 3a. Kerremans, 1892: 102; 1902: 149. Carter, 1929: 282. Obenberger, 1930: 366.

FIG. 22F

Type. Holotype, MNHN (not seen by the author). *Colour.* Head and pronotum dull, elytra shiny. Upper surface and antennae black with blue reflections. The whole upper surface except the antennae speckled with small yellow spots. Undersurface black with yellow spots larger than on the upper surface; hairs silver. Legs dark brown; each femur with a single elongate spot; the tarsi black.

Shape and sculpture. Head with shallow even punctures and a small glabrous spot between the eyes. Pronotum evenly punctured, the punctures larger at the sides than in the middle; slightly inflated after the middle, rounding and narrowing quickly to the apex; the front edge projects forwards in the middle. Elytra with intervals between the striae convex, punctured and wrinkled; laterally slightly concave, rounding well after the middle to the sutural spines which are turned out. Undersurface evenly punctured, but the punctures larger at the sides than in the middle, the differences pronounced on the thorax. Apart from the legs, apical edges of the abdomen and pronotum, the body is devoid of hair.

Size. Males $12.3 \pm 0.73 \times 4.9 \pm 0.3$ mm (7). Females $15.1 \pm 0.95 \times 6.0 \pm 0.35$ mm (6).

Distribution. Western Australia.

Specimens examined. W. Aust.: 1 ♂, Leonora, H. W. Brown, 2.xi.1934, WAM, 34-511; 1 ♀, 80 km S of Coolgardie, Jan. 1937, A. M. Douglas, WAM, 37-722; 1 ♂ & 1 ♀, Taria Rock, 2.i.1940, A. M. Douglas, WAM, 40-32; 40-31; 2 ♂, Watning, 20.ix.1950, R. P. McMillan, WAM, 73-384, 73-386; 2 ♂ & 1 ♀, Watning, 26.xi.1950, R. P. McMillan, WAM, 73-385, 73-388; 1 ♂ & 2 ♀, WAM, 73-375/7; 1 ♀, Red Gum Pass, Stirling Ranges on *Casuarina* sp., 26.i.1971, E. & K. Curaby.

7. *Astraeus (Depollus) irregularis* van de Poll, 1889: 84, 86, 87, pl. 2, fig. 1, 1a. Kerremans, 1892: 102; 1902: 149. Carter, 1929: 282. Obenberger, 1930: 366.

FIG. 22G

Type. Holotype, MNHN (not seen by author.)

Colour. Head and thorax dull, elytra shiny.

Male. Head black with blue reflections, with the following yellow markings: a continuous band under the lower half of the eye; an elongate spot in the centre of the head which may be broken into several spots; two elongate spots lateral and basal to the central spot, each of which may be broken into two spots; a small spot on either side of the gular. Except for the central spot, all other spots may be reduced or absent. Antennae dark brown with blue reflections. Pronotum black with blue reflections and the following yellow markings: a spot on the margin of the apical edge on each side of the middle; a spot on each side below the first, towards the base; two spots along the sides, a small one at the apex and an elongate larger one at the base—the first may be absent and the second broken into two spots. All of these spots may be reduced and some or all of them absent. Elytra black with blue reflections, each elytron with the following yellow markings: the basic pattern is of three spots in the middle but not touching the suture; the first is a small elongate spot at the base; the second a large spot before the middle; the third a vitta after the middle and extending to the pre-apical area; there are also two small elongate spots at the margin, one at the shoulder extending to the region of the humeral fold and a smaller one just behind it which is sometimes absent; an irregular number of small spots are present along the basal edge between the vitta and the suture. Undersurface dark brown with blue reflections; with yellow spots at the base of each leg and single lateral spots on the pro-

sternum, third coxal plate and abdominal segments 1-4, 1-3 or 1-2, decreasing in size from first to last; hairs silver. Legs dark brown with blue reflections.

Female. Head, pronotum and elytra basically similar to the male except that the yellow markings are larger and the irregular spots are more numerous. Undersurface and legs as in the male except that lateral spots are present on all the abdominal segments.

Shape and sculpture. Head broad; with shallow punctures larger at the sides than in the middle and a longitudinal glabrous line between the eyes. Pronotum with shallow punctures larger at the sides than in the middle; the lateral margins rounded and narrowed gently at the base, more abruptly at the apex. Elytra with the intervals between the striae slightly convex, with a shallow row of punctures and faintly transversely wrinkled; parallel-sided until after the middle, then rounded to the sutural spine which is well developed and turned out. Undersurface more closely punctured at the sides than in the middle; with a few short hairs.

Size. Males $11.2 \pm 0.24 \times 4.1 \pm 0.08$ mm (11). Females $13.5 \pm 0.22 \times 4.7 \pm 0.08$ mm (20).

Distribution. Western Australia.

Specimens examined. W. Aust.: 3 ♂ & 5 ♀, Gosnells on *Casuarina* sp., 24.xii.1967, S. Barker; 1 ♂ & 2 ♀, Gosnells on *Casuarina* sp., 27.xii.1967, S. Barker; 2 ♂ & 3 ♀, Red Hill Rd near Midland Junction on *Casuarina* sp., 4.i.1968, S. Barker; 2 ♀, 77 km along main York Rd on *Casuarina* sp., 5.i.1968, S. Barker; 3 ♂ & 4 ♀, South Tammin Flora Reserve on *Casuarina huegeliana*, 6.i.1971, S. Barker; 1 ♂ & 2 ♀, 142 km E of Norseman on *C. huegeliana*, 19.xii.1972, S. Barker; 1 ♀, 58 km W of Tammin on York-Tammin Rd on *C. huegeliana*, 23.xii.1972, S. Barker; 1 ♂ & 1 ♀, 3 km E of Gosnells on *C. huegeliana*, 27.xii.1972, S. Barker.

8. *Astraeus (Depollus) dedariensis* sp. nov.

FIGS 4, 22H

Types.

Holotype: ♂, Dedari, W. Aust., H. W. Brown, WAM, 71-1779.

Allotype: ♀, Dedari, W. Aust., H. W. Brown, WAM, 71-1778.

Paratypes: 2 ♀, Dedari, W. Aust., WAM, 40-1207, 40-1208; 1 ♀, Borden, W. Aust., SAM; 1 ♀, Dedari, W. Aust., ANIC; 1 ♀, Dedari, W. Aust., on *Casuarina variegata*, 21.i.1936, H. W. Brown, MNHN.

Colour, Shiny. Head black with purple reflections and the following yellow markings: an ovoid spot touching the underside of each eye

and pointing downwards but not touching the mouth; a single circular spot in the middle. Antennae brown with blue and purple reflections except for the first segment which is predominantly black. Pronotum black with purple and blue reflections and the following yellow markings: a small ovoid spot on each side at the apex; a larger ovoid spot in the middle of each side at the base, slightly angled outwards on the apical side; laterally there is a line on each side from the apex to the base where it is extended by the flaring outwards of the lateral margin of each lobe exposing the yellow inner surface. Elytra black with purple and blue reflections and the following yellow markings which do not form a symmetrical pattern on each side: a large basal spot; behind and in line a large elongate spot, commencing before the middle and ending at the middle, close to the suture but not touching it; an elongate spot commencing after the middle and running to the apex, close to the suture but not touching it; an elongate spot at the shoulder, not touching the outer margin but close to it; behind the last a much smaller spot, not touching the margin; after the middle there are several elongate spots extending almost to the apex but not touching the outer margin; several small eccentric oval spots. Undersurface black with purple reflections; the first three abdominal segments have lateral yellow spots which progressively diminish in size from in front backwards; hairs silver. Legs: mesosternal and metasternal coxae with yellow spots on the outer margins; the rest brown with purple reflections; the upper surfaces of the tarsi are black.

Shape and sculpture. Head with shallow punctures and without hair. Pronotum with shallow punctures; a short median impressed line projects forwards from the basal crypt; parallel-sided at the base, abruptly rounded at the apex; with short hair on the anterior edge only. Elytra with the intervals between the striae slightly convex and transversely strigose; parallel-sided until after the middle then rounding off to the apex; each ending in a thick short spine projecting backwards; no marginal spine but a small mound is present in the region where they occur in other species. Undersurface with shallow punctures; with a few short hairs.

Size. Males 11.2×4.2 mm (1). Females $13.0 \pm 0.15 \times 5.0 \pm 0.1$ mm (6).

Distribution. Western Australia.

General remarks. This species shows closest affinity with *Astraeus irregularis*.

Specimens examined. Types only.

Sub-genus *Astraeus* (*sensu stricto*) **sub-gen. nov.**

Type-species *Astraeus flavopictus* LaPorte & Gory, 1837.

Description. Head medium sized; with or without a median longitudinal raised ridge between the eyes, the median keel (Fig. 25). Antennae

long. Pronotum deeply notched on both sides at the base, with the median lobe and the two lateral lobes pointed. Elytra striate-punctate and/or costate, the outer edge of the intervals between the striae costate, either down the entire length or towards the apex only. The suture ends posteriorly in a spine and in all but three species these are sharp and curved outwards. The marginal spines are smaller than the sutural spines. The humeral fold is variably developed and angled (Fig. 1).

Key to the species of *Astraeus* (*sensu stricto*)

- | | |
|--|---------------------------------------|
| 1. Head with a median keel | 2 |
| 1. Head without a median keel | 15 |
| 2. Hairs silver | 3 |
| 2. Hairs yellow | 14 |
| 3. Part or all of the anterior undersurface red-brown | 4 |
| 3. None of the anterior undersurface red-brown | 6 |
| 4. Gular, prosternum, meso- and metasternum, 2nd and 3rd coxae and 1st abdominal segment red-brown | 9. <i>bakeri</i> sp. nov. |
| 4. Prosternum and coxae red-brown | 10. <i>minutus</i> sp. nov. |
| 4. A red-brown area on either side of the prosternal process | 5 |
| 5. Usually shorter than 7.5 mm; humeral fold well developed and acutely angled | 11. <i>fraseriensis</i> sp. nov. |
| 5. Usually longer than 7.5 mm; humeral fold moderately developed and angled | 15. <i>obscurus</i> sp. nov. |
| 6. Most of the leg testaceous | 7 |
| 6. Tips of the tibia and 1st tarsal segment testaceous | 8 |
| 6. None of the leg testaceous | 10 |
| 7. 1st and 2nd legs testaceous except for the outer margin of the femur, 3rd leg testaceous except for the femur | 19. <i>dilatipes</i> van de Poll |
| 7. Tibia, 1st and 2nd tarsal segments testaceous | 13. <i>smeythi</i> sp. nov. |
| 8. Usually shorter than 7 mm | 12. <i>pygmaeus</i> van de Poll |
| 8. Usually longer than 7 mm | 9 |
| 9. Humeral fold well developed, acutely angled | 17. <i>mastersi</i> MacLeay |
| 9. Humeral fold well developed and angled | 18. <i>samouelli</i> Saunders |
| 10. Humeral fold moderately developed and angled | 11 |
| 10. Humeral fold poorly developed, slightly angled | 13 |
| 11. Head and pronotum green and coppery-purple | 21. <i>intricatus</i> Carter |
| 11. Head and pronotum black | 12 |
| 12. Broad and rounded species | 16. <i>globosus</i> sp. nov. |
| 12. Elongate species | 35. <i>watsoni</i> sp. nov. |
| 13. Black species; elytral markings a number of yellow spots | 22. <i>crassus</i> van de Poll |
| 13. Blue species; elytral markings two yellow fascia | 25. <i>fraterculus</i> van de Poll |
| 14. Elytral markings three yellow fascia and red areas | 23. <i>major</i> Blackburn |
| 14. Elytral markings two yellow fascia without red areas | 24. <i>navarchis</i> (Thomson) |
| 15. Body elongate and cylindrical | 16 |
| 15. Body not elongate and cylindrical | 17 |
| 16. Pronotum conically elevated in the middle | 26. <i>prothoracicus</i> van de Poll |
| 16. Pronotum not conically elevated in the middle | 27. <i>elongatus</i> van de Poll |
| 17. Sutural spine with a rounded internal edge | 18 |
| 17. Sutural spine with a straight internal edge | 26 |
| 18. Legs a red-brown colour | 19 |
| 18. Legs not a red-brown colour | 20 |
| 19. Elytral markings spots and fascia | 30. <i>macmillani</i> sp. nov. |
| 19. Elytral markings two vittae on each elytron | 28. <i>vittatus</i> van de Poll |
| 20. Head, pronotum and legs metallic brown or bronze | 29. <i>flavopictus</i> LaPorte & Gory |
| 20. Head, pronotum and legs not metallic brown or bronze | 21 |
| 21. Humeral fold well developed and angled | 22 |
| 21. Humeral fold poorly developed, slightly angled | 23 |
| 22. Head black or coppery-purple; undersurface coppery-purple | 20. <i>adamsi</i> sp. nov. |
| 22. Head blue or green; undersurface blue-green | 14. <i>stimulator</i> van de Poll |

23. Basal spot expanded along the front edge of the elytron 31. *carabyi* sp. nov.
 23. Basal spot not expanded along the front margin of the elytron 24
 24. Elytral markings either two spots and two fascia or the first fascia may be broken making four spots and a fascia on each elytron 32. *badeni* van de Poll
 24. Elytral markings either six spots and a fascia or the fascia may be broken making eight spots on each elytron 33. *jansoni* van de Poll
 24. Elytral markings 7 spots on each elytron 25
 25. Pronotum parallel-sided from base to the middle then strongly rounded and narrowed to the apex; dorsally convex in lateral profile 34. *oberthuri* van de Poll
 25. Pronotum gradually rounded at the sides and narrowed from base to apex; dorsally flattened in lateral profile 36. *carteri* sp. nov.
 26. Head slightly excavated between the eyes 37. *goerlingi* sp. nov.
 26. Head deeply excavated between the eyes 27
 27. Head excavated mainly at the base; pronotum laterally inflated with an oval patch of hexagonal cells in the middle 38. *cyaneus* Kerremans
 27. Head excavated mainly at the apex; pronotum not laterally inflated and without hexagonal cells 39. *caledonicus* Fauvel

9. *Astraeus (Astraeus) bakeri* sp. nov.

FIGS 5, 221

Types.

Holotype: ♂, Dryandra, W. Aust. on *Casuarina huegeliana*, 8.xii.1970, S. Barker, SAM, I 20945.

Allotype: ♀, Dryandra, W. Aust. on *C. huegeliana*, 8.xii.1970, S. Barker, SAM, I 20946.

Paratypes: 1 ♂ & 1 ♀, Dryandra, W. Aust. on *C. huegeliana*, 12.i.1973, S. Barker, EA; 2 ♀, Toompup, W. Aust. on *Casuarina* sp., E. & K. Carnaby, KC; 2 ♀, Dryandra, W. Aust. on *Casuarina* sp., 2.i.1968, S. Barker, SAM; 4 ♂ & 4 ♀, Dryandra, W. Aust. on *C. huegeliana*, 8.xii.1970, S. Barker, ANIC (1 ♂ & 1 ♀), BM (1 ♂ & 1 ♀), MNHN (1 ♂ & 1 ♀), WAM (1 ♂ & 1 ♀).

Colour. Shiny. Head and pronotum black with violet or green reflections; antennae black with metallic blue reflections, tips of first and second segments brown. Elytra black with violet reflections, each with the following yellow markings: a spot at the base; a fascia above the middle, covering the humeral fold and ending near the suture but not touching it, broken into spots in some specimens; a large spot below the middle. Undersurface: gular, pro-meso- and metasternum, second and third coxae and median anterior part of the first abdominal segment all reddish-brown with light blue reflections on the lateral part of the above; remaining abdominal segments black with metallic blue reflections; hairs silver. Legs brown with metallic blue reflections on the upper surface, the end of the first tarsal segment and all of the remaining tarsal segments metallic blue.

Shape and sculpture. Head evenly punctured; small median keel; hairy. Pronotum deeply and evenly punctured, with a median longitudinal impressed line at the apex; median

lobe without a basal crypt; sides rounded and narrowed from base to apex; hairy. Elytra costate, the intervals between flat with a prominent row of punctures; at the sides gently rounded from the base to just before the middle then rounded and narrowed to the strong marginal spine; sutural spine robust; humeral fold well developed and angled. Undersurface sparsely punctate in the middle, more closely at the sides; covered with fine hair which is denser at the sides than in the middle.

Size. Males $7.5 \pm 0.07 \times 3.0 \pm 0.03$ mm (44). Females $7.9 \pm 0.12 \times 3.2 \pm 0.06$ mm (23).

Distribution. Western Australia.

General remarks. Named after Dr F. H. Uther Baker.

Specimens examined. W. Aust.: Types; 18 ♂ & 8 ♀, Dryandra, on *Casuarina huegeliana*, 8.xii.1970, S. Barker; 6 ♂ & 1 ♀, 13 km E of Ongerup, on *C. huegeliana*, 11.i.1973, S. Barker; 8 ♂ & 3 ♀, Dryandra, on *C. huegeliana*, 12.i.1973, S. Barker; 1 ♂, Ponier rockhole 70 km S of Balladonia, on *C. huegeliana*, 5.xii.1974, S. Barker; 3 ♂, Juranda rockhole 106 km S of Balladonia, on *C. huegeliana*, 9.xii.1974, S. Barker; 1 ♂, 115 km S of Balladonia on *Casuarina humilis*, 9.xii.1974, S. Barker; 1 ♂, SW valley of Mt Ragged, on *C. huegeliana*, 10.xii.1974, S. Barker; 1 ♀, 3 km S of Mt Ragged on Israelite Bay road, on *C. humilis*, 10.xii.1974, S. Barker.

10. *Astraeus (Astraeus) minutus* sp. nov.

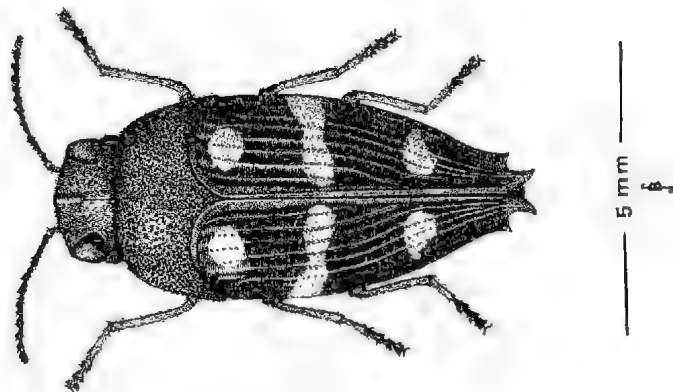
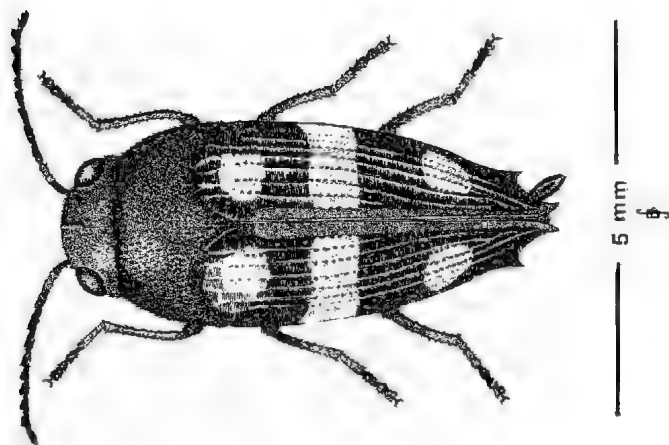
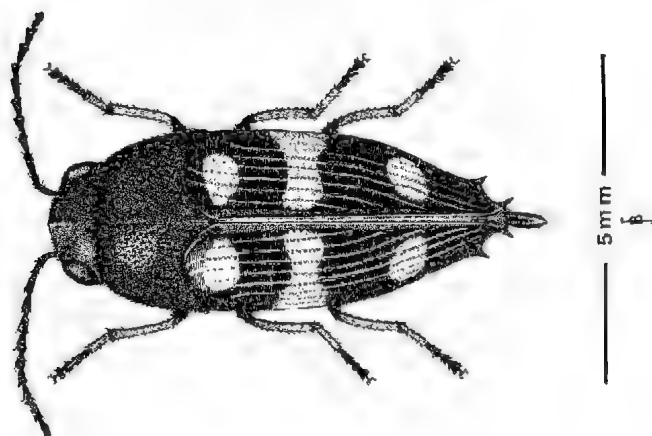
FIGS 6, 221

Types.

Holotype: ♂, South Tammin Flora Reserve, W. Aust. on *Casuarina huegeliana*, 6.i.1971, S. Barker, SAM, I 20459.

Allotype: ♀, South Tammin Flora Reserve, W. Aust. on *C. huegeliana*, 23.xii.1972, S. Barker, SAM, I 20460.

Paratypes: 2 ♂, South Tammin Flora Reserve, W. Aust. on *C. huegeliana*, 23.xii.1972, S. Barker, ANIC (1), MNHN (1); 1 ♂, South

Fig.. 5. *Astraeus bakeri* sp. nov.Fig. 6. *Astraeus minutus* sp. nov.Fig. 7. *Astraeus fraseriensis* sp. nov.

Tammin Flora Reserve, W. Aust. on *C. huegeliana*, 6.i.1971, S. Barker, SAM; 1 ♂, South Tammin Flora Reserve, W. Aust. on *C. huegeliana*, 9.i.1974, S. Barker, BM; 2 ♂, South Tammin Flora Reserve, W. Aust. on *C. campestris*, 9.i.1974, S. Barker, WAM.

Colour. Shiny. Head black with purple reflections; antennae black with blue reflections except for the tips of the first and second segments which are brown. Pronotum black with purple reflections in the middle, red-brown at the sides. Elytra black with purple reflections each with the following yellow markings: a large basal spot; a fascia before the middle covering the humeral fold but not reaching the suture; a large median spot after the middle. Undersurface: prosternum and coxal plates red-brown, the rest black with metallic purple reflections; hairs silver. Legs: upper femur red-brown, the rest of the femur and upper part of the tibia metallic purple; apical part of the tibia and first tarsal segment testaceous; second, third and fourth tarsal segments black with blue reflections.

Shape and sculpture. Head broad; deeply and evenly punctured; with a median keel; hairy. Pronotum deeply and evenly punctured, with a short impressed line projecting forwards from the basal crypt; sides gradually rounded from base to apex; hairy. Elytra costate the intervals flat each with a row of very shallow punctures; laterally tapering gradually from base until after the middle, then rounded to the well-developed marginal spine; a very elongate crescentic emargination between the marginal spine and the well developed sutural spine; humeral fold well developed and acutely angled. Undersurface evenly punctured; hairy.

Size. Males $5.7 \pm 0.22 \times 2.3 \pm 0.10$ mm (7). Females 6.4×2.7 mm (1).

Distribution. Western Australia.

General remarks. The smallest species known at this time.

Specimens examined. Types only.

11. *Astraeus* (*Astraeus*) *fraseriensis* sp. nov.

FIGS 7, 22K, 24, 25

Types.

Holotype: ♂, Fraser Range, W. Aust. on *Casuarina huegeliana*, 19.xii.1972, S. Barker, SAM, 1 20951.

Allotype: ♀, Fraser Range, W. Aust. on *C. huegeliana*, 19.xii.1972, S. Barker, SAM, 1 20952.

Paratypes: 2 ♂ & 2 ♀, Dryandra, W. Aust. on *C. huegeliana*, 12.i.1973, S. Barker, EA (1 ♂ & 1 ♀), MNHN (1 ♂ & 1 ♀); 2 ♂ & 2 ♀, Fraser Range, W. Aust. on *C. huegeliana*

19.xii.1972, S. Barker, ANIC (1 ♂ & 1 ♀), BM (1 ♂ & 1 ♀); 1 ♂, Lake Grace, W. Aust., 9.i.1972, E. & K. Carnaby, KC; 3 ♂, Fyre Highway 142 km E of Norseman, W. Aust. on *C. huegeliana*, 19.xii.1972, S. Barker, SAM; 2 ♂ & 1 ♀, South Tammin Flora Reserve, W. Aust. on *C. huegeliana*, 6.i.1971, S. Barker, WAM.

Colour. Shiny. Head, antennae and pronotum black with violet and blue reflections. Elytra black with purple reflections, each with the following yellow markings: a large basal spot in the middle; a fascia covering the humeral fold, running towards the suture but not touching it, and slightly concave towards the base; a large spot after the middle not touching the suture or the margin; sometimes there is a preapical spot. Undersurface metallic purple except for a red-brown patch on either side of the prosternal process at the anterior edge of the prosternum; hairs silver. Legs: femur metallic purple, tibia and first tarsal segment predominantly testaceous, second, third and fourth tarsal segments dark with blue reflections.

Shape and sculpture. Head closely and evenly punctured; with a median keel; hairy. Pronotum closely and evenly punctured with a slightly excavated median longitudinal line projecting forwards from the basal crypt; rounded at the sides and narrowed from base to apex; hairy. Elytra costate, the intervals between flat, each with a row of punctures; parallel-sided until after the middle then gently rounded and narrowed to the marginal spine; both spines well developed; humeral fold well developed and acutely angled. Undersurface shallowly punctured in the middle, punctures deeper at the sides; hairy.

Size. Males $6.7 \pm 0.05 \times 2.6 \pm 0.02$ mm (72). Females $7.0 \pm 0.08 \times 2.8 \pm 0.04$ mm (28).

Distribution. Western Australia.

General remarks. The three species *Astraeus bakeri*, *Astraeus minutus* and *Astraeus fraseriensis* show a close affinity to each other.

Specimens examined. W. Aust.: Types: 1 ♀, 58 km W of Tammin on York-Tammin Rd, on *Casuarina huegeliana*, 23.xii.1972, S. Barker; 1 ♂, 58 km W of Tammin on York-Tammin Rd, on *C. huegeliana*, 9.i.1974, S. Barker; 2 ♂, South Tammin Flora Reserve, on *C. huegeliana*, 23.xii.1972, S. Barker; 4 ♂ & 2 ♀, South Tammin Flora Reserve, on *C. huegeliana*, 9.i.1974, S. Barker; 31 ♂ & 6 ♀, Coragina rockhole 66 km S of Balladonia, on *C. huegeliana*, 5.xii.1974, S. Barker; 18 ♂ & 13 ♀, Ponier rockhole 70 km S of Balladonia, on *C. huegeliana*, 5.xii.1974, S. Barker; 5 ♂, Juranda rockhole 106 km S of Balladonia, on *C. huegeliana*, 9.xii.1974, S. Barker; 1 ♂, 19

km W of Balladonia, on *C. humilis*, 23.ii.1975, S. Barker.

12. *Astraeus (Astraeus) pygmaeus* van de Poll, 1886: 178-180; 1889: 85, 104, 105, pl. 3, figs 16, 16a, 16c, Blackburn, 1891: 496, van de Poll, 1892: 67, 68, Obenberger, 1930: 366, Carter, 1931: 107; 1933: 41.

Astraeus pygmaeus var. *subfasciatus* van de Poll, 1886: 178-180; 1889: 104, 105, pl. 3, fig. 16b, Obenberger, 1930: 366.

Astraeus maitlandi var. *pygmaeus*, Blackburn, 1890: 1256.

Astraeus samonelli var. *pygmaeus*, Kerremans, 1892: 102.

Astraeus pygmaeus, Kerremans, 1902: 148.

Astraeus pygmaeus var. *subfasciatus*, Kerremans, 1902: 148.

Astraeus pygmaeus, Carter, 1929: 282.

Astraeus pygmaeus var. *subfasciatus*, Carter, 1929: 282.

FIG. 221.

Type. Holotype: ♀, Queensland, MNHN (seen by author).

Colour. Male. Turquoise with golden-green reflections at the apex, dark at the base with purple reflections; antennae dark with blue reflections. Pronotum dark in the middle with golden-green and purple reflections, turquoise at the sides with golden-green reflections. Elytra black with blue reflections, each with the following yellow markings: a spot at the base; a fascia covering the humeral fold, slightly concave towards the base but not touching the suture; a spot after the middle, not touching the margin or the suture. Undersurface metallic turquoise in the middle, metallic blue at the sides; hairs silver. Legs metallic blue; tips of tibia and first tarsal segment testaceous; tarsal segments 2, 3 and 4 dark brown with blue reflections.

Female. Head blue at the apex, dark at the base with purple reflections; antennae black with blue reflections. Pronotum black in the middle with purple reflections, blue at the sides. Elytra as in the male except that the fascia is always broken in the middle to form two spots, and all of the yellow markings are smaller than those in the male. Undersurface deep metallic blue; hairs silver. Legs deep metallic blue; tips of the tibia and first tarsal segment testaceous.

Shape and sculpture. Head evenly and closely punctured; with a median keel; hairy. Pronotum closely punctured, the punctures larger at the sides than in the middle; parallel-sided from the base until just before the middle then rounded and tapered to the apex; hairy. Elytra costate, the intervals flat, each with a row of

punctures and transversely wrinkled; parallel-sided until after the middle then rounded and tapered to the marginal spine; both spines well developed; humeral fold well developed and angled. Undersurface; prosternal punctures larger at the sides than in the middle, punctures uniform on the abdomen; hairy.

Size. Males $6.2 \pm 0.05 \times 2.5 \pm 0.02$ mm (66). Females $6.6 \pm 0.08 \times 2.6 \pm 0.04$ mm (40).

Distribution. Queensland and New South Wales.

Specimens examined. Qld.: Type: 1 ♂ & 1 ♀, Edungalba on *Casuarina* sp., 14.xi.1971, E. E. Adams; 8 ♂ & 4 ♀, Edungalba on *Casuarina* sp., 9.xi.1974, E. E. & S. Adams; 1 ♂ & 1 ♀, Edungalba on *Casuarina* sp., 15.xii.1974, E. E. & S. Adams. N.S.W.: 41 ♂ & 19 ♀, Oranmeir on *Casuarina littoralis*, 9.xii.1962, S. Barker; 2 ♂ & 2 ♀, Major's Creek on *C. littoralis*, 26.i.1963, S. Barker. A.C.T.: 3 ♂ & 1 ♀, Mt Ainslie on *Casuarina stricta*, 29.xi.1962, S. Barker; 6 ♂ & 2 ♀, Mt Ainslie on *C. stricta*, 26.xii.1962, S. Barker; 4 ♂ & 3 ♀, Tuggeranong on *C. stricta*, 13.1963, S. Barker.

13. *Astraeus (Astraeus) smythi* sp. nov.

FIGS 8, 22M

Types.

Holotype: ♂, Maryborough, Qld, November 1956, E. Smith, WAM, 73-55.

Allotype: ♀, WAM, 73-56.

Paratypes: 2 ♀, Qld, E. Sutton, QM; 1 ♂, SAM.

Colour. Male. Head: apex blue with golden-green reflections, base dark blue with purple reflections; antennae black with blue and purple reflections. Pronotum black in the middle with purple reflections, blue at the sides with golden-green reflections. Elytra black with purple reflections each with the following yellow markings: a spot at the base; a broad fascia covering the humeral fold, running transversely towards the suture but not touching it; a fascia commencing after the middle at the margin, running transversely to the suture but not touching it. Undersurface metallic blue; hairs silver. Legs metallic blue; tibia and first and second tarsal segments testaceous; third and fourth tarsal segments dark brown. A small preapical spot may or may not be present.

Female. Head: apex turquoise, base green; antennae black with blue and green reflections. Pronotum green in the middle, turquoise at the sides. Elytra black with blue and purple reflections, yellow markings as described in the male but less prominent. Undersurface and legs as in the male.

Shape and sculpture. Head evenly punctured; a median keel; hairy. Pronotum with punctures larger at the sides than in the middle; a faint longitudinal impressed line commences at the middle and runs to the apex; parallel-sided from the base to just before the middle then rounded and tapered to the apex. Elytra costate, the intervals between flat each with a row of punctures and faintly transversely wrinkled; parallel-sided until before the middle, then rounded and tapered to the marginal spine; both spines well developed; humeral fold well developed and angled. Undersurface: prosternal punctures shallow in the centre, deeper at the sides; punctures on the abdominal sternites sparser and shallower; hairy.

Size. Males $6.5 \pm 0.08 \times 2.6 \pm 0.15$ mm (2). Females $6.5 \pm 0.18 \times 2.6 \pm 0.01$ mm (4).

Distribution. Queensland.

General remarks. *A. smythi* shows close affinity with *A. pygmaeus*. I place these species alongside the previous group of three species. Named after my late colleague, Dr M. Smyth.

Specimens examined. Qld.: Types: 1 ♀, One Tree Hill, Brisbane, 1920, R. Muir, BPBM.

14, *Astraeus (Astraeus) simulator* van de Poll, 1889: 85, 102, 104, pl. 3, figs 15, 15a, 15b. Kerremans, 1892: 102, 1902: 148. Carter, 1929: 282. Ohenberger, 1930: 366.

FIG. 22N

Type. Holotype: ♀, Peak Downs, MNHN (seen by author).

Colour. **Male.** Shiny. Head green at the apex with golden-green reflections, black at the base with blue reflections; antennae black with golden-green and blue reflections. Pronotum black with blue and purple reflections. Elytra black with turquoise reflections, each with the following markings: a large basal spot; a fascia covering the humeral fold, running transversely towards the suture but not touching it, concave towards the base and clubbed at the end; a fascia after the middle running transversely from the margin but not touching the suture. Undersurface metallic blue; hairs silver. Legs metallic blue; tips of tibia and first tarsal segment brown; second, third and fourth tarsal segments black with blue reflections.

Female. Head black with blue reflections; antennae black with blue-green reflections. Pronotum black with blue reflections. Elytra black with blue and purple reflections. The rest as in the male.

Shape and sculpture. Head with close uniform punctures; no median keel; hairy. Pronotum evenly punctured; basal third parallel-sided then slightly rounded and narrowed to the apex; anterior margin projecting forward in the middle, that general area glabrous; hairy. Elytra costate, the intervals between flat but slightly wrinkled; parallel-sided from the base, rounded before the middle then tapering to the marginal spine; both spines well developed; humeral fold well developed and angled. Undersurface evenly punctured; hairy.

Size. Males $6.7 \pm 0.10 \times 2.5 \pm 0.05$ mm (11). Females $7.0 \pm 0.24 \times 2.7 \pm 0.09$ mm (6).

Distribution. Queensland.

General remarks. Of the 17 specimens I have examined, 7 ♂ and 2 ♀ have preapical spots on the elytra, the other eight specimens have no preapical spots. Although male genitalia (Fig. 22N) is similar in shape to the previous two groups of species, the external morphology of *A. simulator* is dissimilar to those five species. Because of this I do not group it with any of the above mentioned species.

Specimens examined. Qld.: Type: 1 ♂, 3.xii.1971, E. E. Adams, KC; 4 ♂ & 1 ♀, Edungalba on *Casuarina equisetifolia*, 11.xii.1973, E. E. Adams, SAM (1 ♂ & 1 ♀), EA (3); 1 ♀, Edungalba on *C. equisetifolia*, 15.xii.1973, E. E. Adams, EA; 2 ♂, Edungalba on *Casuarina* sp., 1 on each of 23.xi.1974 and 8.xii.1974, E. E. & S. Adams, EA; 1 ♀, Edungalba on *Casuarina* sp., 30.xi.1974, E. E. & S. Adams, EA; 2 ♂ & 2 ♀, Edungalba on *Casuarina* sp., 14.xii.1974, E. E. & S. Adams, EA; 2 ♂, Edungalba on *Casuarina* sp., 15.xii.1974, E. E. & S. Adams, EA.

15. *Astraeus (Astraeus) obscurus* sp. nov.

FIGS 9, 22O

Types.

Holotype: ♂, Fraser Range, W. Aust., on *Casuarina heugeliana*, 19.xii.1972, S. Barker, SAM, I 20957.

Allotype: ♀, Fraser Range, W. Aust., on *C. heugeliana*, 19.xii.1972, S. Barker, SAM, I 20958.

Paratypes: 2 ♂ & 2 ♀, Eyre Highway 142 km E of Norseman, W. Aust. on *C. heugeliana*, 19.xii.1972, S. Barker, EA (1 ♂ & 1 ♀), ANIC (1 ♂ & 1 ♀); 2 ♂ & 2 ♀, Fraser Range, W. Aust. on *C. heugeliana*, 19.xii.1972, S. Barker, BM (1 ♂ & 1 ♀), MNHN (1 ♂ & 1 ♀); 1 ♂, 24 km NE of Lake Grace, W. Aust., on *C. heugeliana*, 24.i.1973, S. Barker, KC; 1 ♂, Tammin, W. Aust., H. W. Brown, WADA; 1 ♀, 2 km N of Needilup, W. Aust., 23.xii.1972, K. Newby, WADA; 1 ♀, 30 km W of No. 8 pumping station (Kalgoorlie water main) on *Casuarina campestris*, 24.i.1958, WAM, 71-1775; 1 ♀, WAM, 71-1777; 1 ♀, South Tammin Flora Reserve on *C. heugeliana*, 23.xii.1972, S. Barker, WAM.

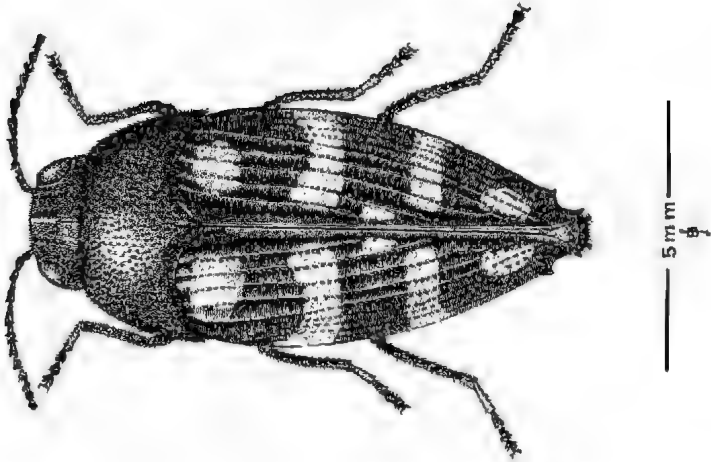


Fig. 10, *Astraeus globosus* sp. nov.

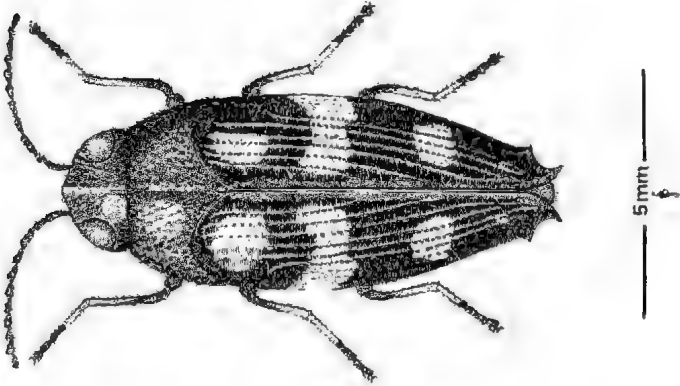


Fig. 9, *Astraeus obscurus* sp. nov.

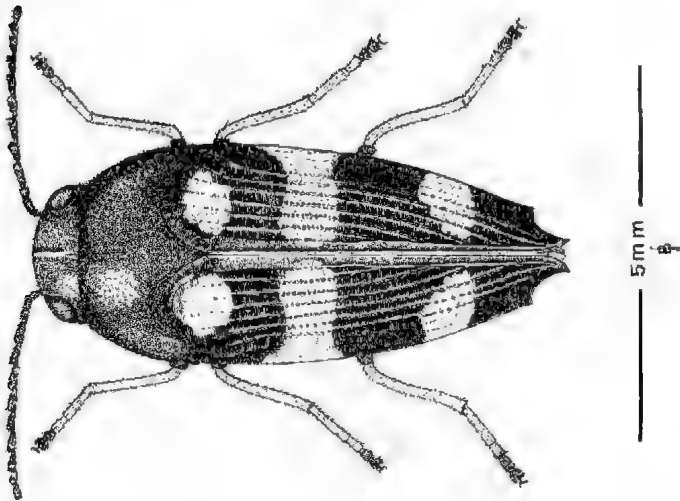


Fig. 8., *Astraeus smythi* sp. nov.

Colour. Shiny. Head purple or black with metallic purple reflections at the apex, metallic blue reflections at the sides and underneath; antennae black with blue and purple reflections, tips of first, second and third segments dark brown. Pronotum purple or black with metallic blue reflections at the sides. Elytra black with blue and purple reflections each with the following yellow markings: a large round basal spot; a broad fascia before the middle concave towards the base commencing at the outer margin, enclosing the humeral fold, running towards the suture but not touching it; a broad fascia after the middle but not touching the outer margin or the suture; a very small preapical spot in the form of a lunette sometimes missing. Undersurface black with purple reflections, except for a red-brown patch on either side of the prosternal process extending to the lateral margin; hairs silver. Legs: femur, basal half of the tibia and second, third and fourth tarsal segments dark brown with blue and purple reflections, apical half of the tibia and first tarsal segment brown.

Shape and sculpture. Head evenly punctured; a large median keel; hairy. Pronotum deeply punctured; a short impressed line projects forward from the basal crypt, becoming a groove and extending to the apex; short with rounded sides gradually narrowing from base to apex; hairy. Elytra costate, the intervals between flat each with a row of shallow punctures; more or less parallel-sided until before the middle then rounded and narrowed to the marginal spine; both spines well developed; humeral fold moderately developed and angled. Undersurface evenly and shallowly punctured; hairy.

Size. Males $9.1 \pm 0.05 \times 3.4 \pm 0.02$ mm (105). Females $9.2 \pm 0.08 \times 3.4 \pm 0.03$ mm (64).

Distribution. Western Australia.

Specimens examined. W. Aust.: Types: 2 ♂ & 2 ♀, Dedari, H. W. Brown, WAM, 71-1771/4; 1 ♂, Spencer's Brook, 26.xii.1946, R. P. McMillan, WAM, 71-1764; 1 ♀, Bejoording, 16.i.1949, WAM, 71-1769; 3 ♂ & 1 ♀, Bejoording, 29.xi.1950, R. P. McMillan, WAM, 71-1765/8; 1 ♂, 11 km E of No. 8 pumping station (Kalgoorlie water main) on *Casuarina campestris*, 20.i.1958, WAM, 71-1776; 33 ♂ & 21 ♀, Coragina rockhole 66 km S of Balladonia on *Casuarina huegeliana*, 5.xii.1974, S. Barker, 21 ♂ & 13 ♀, Ponier rockhole 70 km S of Balladonia on *C. huegeliana*, 5.xii.1974, S. Barker, 14 ♂ & 3 ♀, Juranda rockhole 106 km S of Balladonia on *C. huegeliana*, 9.xii.1974, S. Barker, 3 ♂ & 2 ♀, 115 km S of Balladonia on *Casuarina humilis*, 9.xii.1974, S. Barker.

16. *Astraeus* (*Astraeus*) *globosus* sp. nov.

FIGS 10, 22P

Types.

Holotype: ♂, 77 km along main York Rd. W. Aust. on *Casuarina huegeliana* 5.i.1968, S. Barker, SAM, I 20953.

Allotype: ♀, 77 km along main York Rd. W. Aust. on *C. huegeliana*, 1.i.1968, S. Barker, SAM, I 20954.

Paratypes: 2 ♂ & 1 ♀, Dryandra, W. Aust. on *C. huegeliana* 12.i.1973, S. Barker, EA; 3 ♂ & 2 ♀, Dryandra, W. Aust. on *C. huegeliana*, 8.xii.1970, S. Barker, ANIC (1 ♂ & 1 ♀), MNHN (1 ♂ & 1 ♀), WAM (1 ♂); 1 ♂, 77 km along main York Rd. W. Aust. on *C. huegeliana*, 7.xii.1970, S. Barker, BM; 2 ♂, Toompup, W. Aust. on *Casuarina* sp., 23.i.1972, E. & K. Carnaby, KC; 1 ♀, 77 km along main York Rd. W. Aust. on *Casuarina* sp., 1.i.1968, S. Barker, SAM; 1 ♂, Tutanning Reserve, W. Aust. on *Casuarina* sp., 1.i.1968, S. Barker, SAM; 1 ♀, Spencer's Brook, W. Aust., 26.xii.1945, R. P. McMillan, WAM, 71-1763.

Colour. Shiny. Head and pronotum and elytra black with coppery reflections; antennae black with coppery and blue reflections. Elytra: each elytron with the following yellow markings: a large spot at the base; a broad fascia before the middle, commencing at the shoulder and ending near the suture but not touching it, concave towards the base; a second fascia after the middle, commencing at the margin but not reaching the suture; an oval preapical spot; a single very small spot between the two fascia and close to the suture. Undersurface metallic coppery; hairs silver. Legs: femur metallic coppery, tibia and tarsi brown with varying amounts of metallic blue on the femora and tibia and on the upper surface of the tarsi.

Shape and sculpture. Head closely punctured; with a median keel; hairy. Pronotum deeply punctured but more closely at the sides than in the middle; short with rounded sides narrowed towards the apex; a short impressed line projects forwards from the basal crypt; hairy. Elytra costate, the intervals flat each with a row of shallow punctures; rounded, diverging slightly from the base to a maximum width before the middle, thereafter rounding off to the marginal spine; both spines well developed; humeral fold moderately developed and angled. Undersurface: finely and sparsely punctured in the middle of the sternal segments, more coarsely and closely punctured at the sides; abdominal sternites finely and closely punctured; hairy.

Size. Males $9.4 \pm 0.13 \times 3.6 \pm 0.05$ mm (23). Females $9.3 \pm 0.3 \times 3.9 \pm 0.15$ mm (7).

Distribution. Western Australia.

General remarks. This species shows closest affinity with *A. obscurus*.

Specimens examined. W. Aust. Type: 1 ♂, 77 km along main York Rd on *Casuarina* sp., 5.i.1968, S. Barker; 2 ♂, 77 km along main York Rd on *Casuarina huegeliana*, 7.xii.1970, S. Barker; 1 ♂, *Dryandra* on *C. huegeliana*, 7.xi.1970, S. Barker; 9 ♂ & 1 ♀, *Dryandra* on *C. huegeliana*, 8.xii.1970, S. Barker.

17. *Astraeus (Astraeus) mastersi* Macleay, 1873: 239. Kerremans, 1885: 136. Masters, 1886: 71. Kerremans, 1892: 102.

Astraeus samouelli: van de Poll, 1886: 176, 1889: 80, 107-109, pl. 3, fig. 18b. Kerremans, 1902: 148. Carter, 1929: 282. Obenberger, 1930: 366.

Astraeus splendens van de Poll, 1889: 86, 108, 109, pl. 3, figs 19, 19a. Kerremans, 1892: 102; 1902: 148. Carter, 1929: 282, pl. 3, fig. 43. Obenberger, 1930: 367 (new synonym).

Astraeus simplex Blackburn, 1892: 211, 212. Kerremans, 1902: 149. Carter, 1929: 282. Obenberger, 1930: 366 (new synonym).

FIGS 18, 22Q

Type. Holotype: ♀, Gayndah, AM. X32099 (seen by author).

Colour. Male. Shiny. Head and antennae golden-coppery. Pronotum copper coloured in the middle at the apex, with a dark blue heart-shaped area in the middle, outlined by a copper coloured margin; at the sides, blue at the base green at the apex. Elytra black with blue or purple reflections, each elytron with the following yellow markings: a large spot at the base; a broad fascia running from the shoulder covering the humeral fold and running transversely towards the suture but not reaching it; after the middle a broad fascia from the margin running towards the suture but not reaching it; a preapical spot—in some specimens the preapical spot is absent and usually in these the first fascia is broken in the middle forming two spots. Undersurface blue; hairs silver. Legs: blue; the end of the tibia and first tarsal segment testaceous.

Female. Shiny. Head blue-green at the apex, dark at the base and sides with purple reflections; antennae black with blue or purple reflections. Pronotum dark blue in the middle, metallic blue at the sides. Elytra black with purple reflections, each with the following yellow markings: a large spot at the base; a lateral fascia commencing at the margin and covering the humeral fold, running towards the suture but interrupted to form a spot near the

suture; a small spot near the base, at the shoulder, may or may not be continuous with the base of the fascia; after the middle a fascia running transversely from the margin towards the suture but not touching it; a preapical spot. Undersurface blue with metallic gleams; hairs silver. Legs metallic blue; tips of tibia and first tarsal segment testaceous.

Shape and sculpture. Head shallowly, closely but uniformly punctured; with a median keel; hairy. Pronotum shallowly punctured with punctures larger at the sides than in the middle; a median longitudinal excavated line from base to apex; straight sided from the base to the middle then rounded and narrowed to the apex; hairy. Elytra costate, the intervals flat but slightly wrinkled each with a row of punctures; more or less parallel-sided to before the middle, rounded at the middle then tapering to the marginal spine; both spines well developed; humeral fold well developed and acutely angled. Undersurface with shallow uniform punctures except in the middle and on the outer edges of the abdominal sternites, both areas being glabrous; hairy.

Size. Males $7.9 \pm 0.16 \times 2.7 \pm 0.22$ mm (17). Females $8.4 \pm 0.26 \times 3.2 \pm 0.10$ mm (10).

Distribution. Queensland and northern New South Wales.

General remarks. This is the only species of *Astraeus* that has been greatly confused (see van de Poll 1889, p. 79). The basic reason for this is that the females of *A. mastersi* and *A. samouelli* are very similar in pattern although the males of these species are quite distinct. Both species were described from female types. The lack of field collecting experience was the most likely reason for van de Poll redescribing the male of *A. mastersi* as *A. splendens*, as he would not have had access to an associated series of males and females of the two species.

Specimens examined. N.S.W.: Type; 1 ♂ paratype. Ash L., ANIC: 1 ♂ & 1 ♀ paratype, Gayndah. ANIC: Qld: Type; ♂ *A. splendens* van de Poll, Rockhampton; 3 ♀, Dalby, Mrs. F. H. Hahler. SAM: 1 ♀, Stamburpe, A. Gemmell; 14 ♂ & 5 ♀, Edungalba on *Casuarina equisetifolia*, 24.x.1971. E. E. Adams. Type ♀, *A. simplex* Blackburn NM (locality of collection uncertain).

18. *Astraeus (Astraeus) samouelli* Saunders, 1868: 10, pl. 1, fig. 12; 1871: 43. Masters, 1871: 124. Kerremans, 1885: 136. van de Poll, 1886: 176, 178; 1889: 86, 107, pl. 3, figs 18, 18a. Blackburn, 1891: 496. Kerremans, 1892: 102. van de

Poll, 1892: 67, Blackburn, 1892: 212, Kerremans, 1902: 148, Carter, 1929: 282, *Astracus samouellei*: Gemminger & de Harold, 1869: 1380, Masters, 1886: 71, Blackburn, 1890: 1256, Obenberger, 1930: 366, *Astracus samouellei*: Kerremans, 1900: 295, *Astracus splendens* var. *embrikiellus* Obenberger, 1936: 133.

FIGS 1b, 22R

Type. Holotype: ♀ BM (seen by author).

Colour. Male. Shiny. Head golden-green, golden or coppery; antennae coppery or turquoise. Pronotum uniformly golden-green or golden or coppery in the middle then golden-green blending into turquoise at the sides. Elytra black with blue reflections, each with the following yellow markings: a large spot at the base; a fascia just before the middle covering the humeral fold, extending backwards then transversely towards the suture but not touching it; a spot at the shoulder which may be discrete or continuous with the base of the first fascia; a fascia after the middle, commencing at the margin and running towards the suture but not touching it; variably, a small elongate spot between the two fascia closer to the first and near the suture but not touching it; a preapical spot. Undersurface blue-green; hairs silver. Legs blue-green; tips of the tibia and most of the first tarsal segment testaceous.

Female. Shiny. Head green at the apex with golden reflections, dark blue with purple reflections in the middle of the base, turquoise at the sides; antennae green. Pronotum dark blue with purple reflections in the middle, turquoise at the sides. Elytra black with blue reflections, with markings as in the male except that the first fascia is broken in the middle to form a marginal fascia and a spot near the suture. Undersurface turquoise; hairs silver. Legs turquoise; tips of the tibia and most of the basal part of the first tarsal segment testaceous.

Shape and sculpture. Head shallowly, closely but uniformly punctured; with a median keel; hairy. Pronotum shallowly, closely but uniformly punctured; with a median longitudinal excavated line; uniformly rounded and narrowed from base to apex; very hairy. Elytra costate, the intervals between flat; slightly tapered from the base to the middle, then rounded and tapered to the marginal spine; both spines well developed. Undersurface shallowly punctured, more closely at the sides, less so in the middle; midsurface glabrous; hairy.

Size. Males $8.6 \pm 0.07 \times 3.0 \pm 0.03$ mm (52).

Females $9.2 \pm 0.14 \times 3.3 \pm 0.06$ mm (40).

General remarks. The type of *A. splendens* var. *embrikiellus* Obenberger is a ♀ specimen of *A. samouellei*. This species shows closest affinity with *A. mastersi*.

Distribution. New South Wales.

Specimens examined. N.S.W.: Type: 2 ♂ & 3 ♀, Bredbo on *Casuarina stricta*, 8.i.1963, S. Barker; 12 ♂ & 20 ♀, Major's Creek on *Cosmibuca littoralis*, 26.i.1963, S. Barker; 8 ♂ & 2 ♀, Khanyun Station, Minuma Range on *C. littoralis*, 9.ii.1963, S. Barker; 4 ♂ & 2 ♀, Captains Flat to Braidwood Rd, on *C. littoralis*, 9.ii.1963, S. Barker; Type ♀ *A. splendens* var. *embrikiellus* Obenberger, Comara, NMP, 21.8.89, A.C.T.: 4♂, Mt Ainslie on *C. stricta*, 26.xii.1962, S. Barker; 7 ♂ & 12 ♀, Tuggeranong on *C. stricta*, 1.xii.1962, S. Barker; 3 ♂ & 8 ♀, Tuggeranong on *C. stricta*, 2.xii.1962, S. Barker; 4 ♂ & 2 ♀, Tuggeranong on *C. stricta*, 1.i.1963, S. Barker.

19. *Astracus (Astracus) dilutipes* van de Poll, 1889: 86, 105, 106, pl. 3, fig. 17, 17a, Blackburn, 1892: 212, Kerremans, 1892: 101, 1902: 148, Carter, 1929: 282, Obenberger, 1930: 365.

Astracus samouellei var. *dilutipes* van de Poll, 1886: 180.

Astracus strausi Obenberger, 1928: 205; Carter, 1929: 302, Obenberger, 1930: 367 (new synonym).

FIG. 22S

Type. Holotype, MNHN (not seen by author).

Colour. Male. Shiny. Head green at the apex and golden green at the base or golden-green at the apex and coppery at the base; antennae black with blue reflections. Pronotum divided in a transverse direction by an M-shaped line: the small apical part being green or golden-green, the larger basal part being dark blue or black and the line of demarcation, purple or coppery. Elytra black with blue reflections each with the following yellow markings: in the middle but not touching the suture there is: a large basal spot; a spot before the middle; a preapical spot. On the margin: a large spot covering the humeral fold; after the middle a transverse fascia not touching the suture. Undersurface blue or green; hairs silver. Legs: first and second femora brown on the outer margins, third femur totally or partially solid colour similar to the rest of the undersurface; remainder of leg and tarsi testaceous.

Female. Head green at the apex, purple in the middle, dark blue at the base with purple reflections; antennae black with blue reflections. Pronotum black in the centre with purple and blue reflections, blue at the sides. Elytra as in the male. Undersurface dark blue;

hairs silver. Legs: outer margin of femora brown, tibia and tarsi testaceous.

Shape and sculpture. Head very densely and evenly covered with deep punctures; with a thin median keel; covered with long hair. Pronotum evenly punctured, the punctures at the sides larger than those in the middle; slightly rounded but narrowed from base to apex; median excavated line from base to apex; hairy. Elytra costate, the intervals flat with a row of deep punctures and faintly transversely strigose; narrowed from base until after the middle then rounded and again narrowed to the marginal spine; both spines moderately developed; humeral fold well developed and angled. Undersurface evenly and shallowly punctured; with long hairs.

Size. Males $8.9 \pm 0.21 \times 3.1 \pm 0.08$ mm (11). Females $9.4 \pm 0.13 \times 3.4 \pm 0.07$ mm (7).

Distribution. New South Wales and Queensland.

General remarks. The type of *A. strandi* Obenberger is a small ♀ specimen of *A. dilutipes*. The external morphology of this species is like that of *A. mustersi* and *A. samouelli* but male genitalia (Fig. 22S) is different. I do not group it with the other two species.

Specimens examined. N.S.W.: 9 ♂ & 5 ♀, Major's Creek on *Casuarina littoralis*, 26.i.1963, S. Barker. Qld: 2 ♂ & 2 ♀, Paluma on *Casuarina* sp., 13.i.1970, E. E. Adams; Type ♀ *A. strandi* Obenberger, NMP, 21991.

20. *Astraeus (Astraeus) adamsi* sp. nov.

FIGS 11, 22I

Type.

Holotype: ♂, Edungalba, Qld on *Casuarina equisetifolia*, 30.xi.1974, E. & S. Adams, SAM, I 20944.

Allotype: ♀, Edungalba, Qld on *C. equisetifolia*, 15.xii.1973, E. E. Adams, SAM, I 20939.

Paratypes: 3 ♂ & 3 ♀, Edungalba, Qld on *C. equisetifolia*, 15.xii.1974, E. & S. Adams, EA (1 ♂ & 1 ♀), ANIC (1 ♂ & 1 ♀), BM (1 ♂ & 1 ♀); 1 ♂ & 1 ♀, Edungalba, Qld on *C. equisetifolia*, 23.xi.1974 & 8.xii.1974, E. & S. Adams, MNHN; 1 ♂ & 4 ♀, Edungalba, Qld on *C. equisetifolia*, 14.xii.1974, E. & S. Adams, SAM.

Colour. Shiny. Head black with purple reflections or coppery-purple with metallic reflections. Pronotum black with purple reflections or bronze in the middle, coppery purple at the sides with metallic reflections. Elytra black, with blue and purple reflections, each elytron with the following yellow markings: a basal spot; a spot covering the humeral fold but not reaching the shoulder; a large spot in the

middle not touching the suture and just behind the second spot, these last two in the form of a broken fascia; just behind the break, near the margin but not touching it, there is a small spot (not present in a third of the specimens examined); after the middle a fascia concave backwards commencing at the margin but not reaching the suture; a small preapical spot. Undersurface coppery-purple; legs pale brown, the basal ends of the tibia darker; hairs silver.

Shape and sculpture. Head closely and evenly punctured; no median keel; lightly haired. Pronotum closely and evenly punctured except for a short glabrous line in the middle at the apex; at the sides gradually rounded and narrowed from base to apex. Elytra costate, each interval with a row of deep punctures and faintly transversely wrinkled; parallel-sided to just before the middle then rounded and tapered to the sharp marginal spine; sutural spine well developed; humeral fold well developed and angled. Undersurface closely and evenly punctured, the punctures shallower on the prosternal process than elsewhere; lightly haired.

Size. Males $7.1 \pm 0.14 \times 2.9 \pm 0.05$ mm (6). Females $7.7 \pm 0.10 \times 3.2 \pm 0.04$ (9).

Distribution. Queensland.

General remarks. Male genitalia (Fig. 22T) of *A. adamsi* is similar to that of *A. dilutipes* but external morphology is different. I do not group these two species. Named after Mr E. E. Adams.

Specimens examined. Types only.

21. *Astraeus (Astraeus) intricatus* Carter, 1925: 229, fig. 1; 1929: 282. Obenberger, 1930: 366.

FIGS 1c, 12, 23A

Type. Holotype: ♂, Monaro, VM (seen by author).

Colour. Shiny. Head metallic green at the apex and sides; purple at the base; antennae black with coppery-purple reflections. Pronotum metallic purple in the middle, deep coppery-purple at the sides. Elytra black with purple reflections, each elytron with the following yellow markings: a basal spot, a spot at the middle and a spot after the middle, all elongate and decreasing in size from in front backwards, each with the basal end diverging outwards and all in line to give the appearance of a single, broken vitta with the basal end diverging outwards and the apical end converging to the suture, but not touching it; a fascia commencing at the shoulder, covering

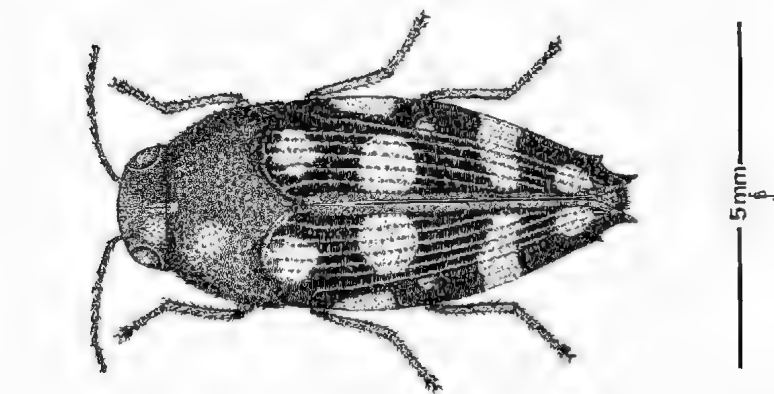


Fig. 11. *Astraeus adamsi* sp. nov.

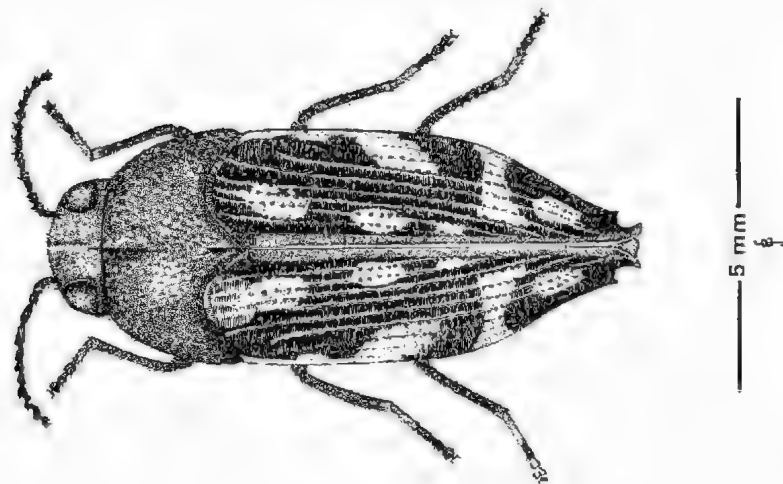


Fig. 12. *Astraeus intricatus* Carter

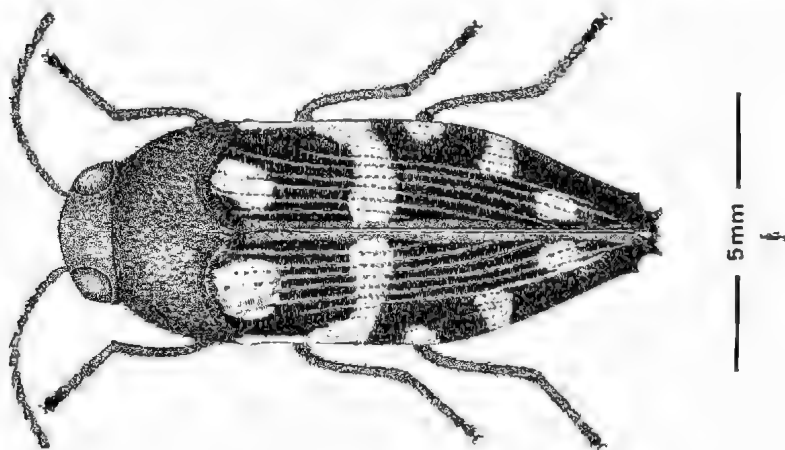


Fig. 13. *Astraeus macmillani* sp. nov.

the humeral fold and running along the outer margin to the middle then extending obliquely towards the suture, reaching slightly below but not touching the middle of the three median spots; after the middle a fascia commencing at the outer margin and running transversely towards the suture but not touching it; an elongate preapical spot, close to the suture but not touching it. Undersurface deep coppery-purple; hairs silver. Legs deep coppery-purple, ends of the tibia, first and second tarsal segments brown, third and fourth tarsal segments dark brown.

Shape and sculpture. Head closely punctured; with a median keel; hairy. Pronotum more closely punctured at the sides than in the middle, with a median longitudinal impressed line visible at the base and apex only; parallel-sided at the base, gently rounded until after the middle, strongly rounded and narrowed to the apex, projecting forward slightly in the middle of the apical edge; hairy. Elytra costate, the intervals between flat, each with a row of shallow punctures; parallel-sided from the base, rounded off well after the middle and narrowed strongly to the marginal spine; both spines well developed; humeral fold moderately developed and angled. Undersurface: sternal segments finely and sparsely punctate in the middle, deeper and larger punctures at the sides; abdominal sternites finely and closely punctured; hairy.

Size. Males $9.6 \pm 0.10 \times 3.5 \pm 0.05$ mm (50). Females $9.8 \pm 0.15 \times 3.6 \pm 0.07$ mm (35).

Distribution. New South Wales.

General remarks. The species was described by Carter from a unique specimen in the MacLeay Museum. Only two of the 85 specimens I have collected conform to the colour pattern of the type. The pattern on the elytra is variable, ranging from the basic pattern as described herein (nine specimens) to patterns in which all of the yellow markings are confluent, giving the appearance of yellow elytra with black borders. Between the extremes, intermediary patterns occur, including the intricate pattern of Carter's type. There is no difference between the sexes in size or colour pattern. All of the specimens I collected were taken on low *Casuarina nana* heath in the Minima and Kybean Ranges, Monaro District, N.S.W. I do not group *A. intricatus* with any other species.

Specimens examined. N.S.W.: Type; 5 ♂ & 10 ♀, Oranmeir on *Casuarina nana*, 9.xii.1962, S. Bar-

ker; 23 ♂ & 9 ♀, Oranmeir on *C. nana*, 26.i.1963, S. Barker; 3 ♂, 16 km S of Countegany Station on *C. nana*, 3.ii.1963, S. Barker; 20 ♂ & 15 ♀, Khanyunis Station on *C. nana*, 9.ii.1963, S. Barker.

22, *Astracrus (Astracrus) crassus* van de Poll, 1889: 85, 95-97, pl. 2, fig. 9, 9a; Kerremans, 1892: 101; 1902: 148. Carter, 1929: 282, Oberberger, 1930: 365.

Astracrus flavopictus van de Poll, 1886: 180.

FIG. 23B

Type. Holotype, MNHN (not seen by author).

Colour. Shiny. Head and pronotum black with purple or blue and purple reflections; antennae black with blue and purple reflections. Elytra black with blue and purple reflections each with the following yellow markings: the basic pattern consists of irregular spots in two rows; four spots in the middle near the suture, but not touching it, one at the base, one before the middle, one after the middle and one in the preapical area; three spots along the margin, one at the shoulder and covering the humeral fold, one at the middle and one after the middle; there may also be a few irregular spots and in two specimens there are spots at the base of the sutural spine. Undersurface and legs black with blue and purple reflections; hairs silver.

Shape and sculpture. Head with a median keel; evenly punctured; hairy. Pronotum with small and sparse punctures in the middle leaving glabrous areas, larger and more dense at the sides with a short impressed line projecting forwards from the basal crypt; gently rounded and narrowed at the sides from the base to two-thirds way to the apex, then tapered to the apex with the apical edge projecting slightly in the middle. Elytra punctate-striate with the intervals flat towards the base and slightly concave towards the apex, each with a row of shallow punctures; parallel-sided until after the middle, then gently rounded and narrowed to the small marginal spine; sutural spine well developed; humeral fold poorly developed but slightly angled. Undersurface shallowly punctured, more closely at the sides than in the middle; hairy.

Size. Males $14.4 \pm 0.25 \times 5.3 \pm 0.06$ mm (5). Females $16.2 \pm 0.40 \times 6.3 \pm 0.15$ mm (7).

Distribution. Queensland and New South Wales.

General remarks. This species cannot be grouped with any other.

Specimens examined. Qld: 1 ♂, E. Sutton, N.S.W.: 1 ♂ & 1 ♀, Sydney, SAM; 1 ♀, Griffith, SAM; 1 ♀, Jenolan Caves, J. C. Wilburd, SAM; 1 ♀, J. G. Tepper, SAM; 1 ♀, Sydney, W. du Boulay, SAM; 1 ♀, W. du Boulay, SAM; 1 ♀, SAM; 2 ♂, Majers Creek on *Casuarina littoralis*, 26.1.1963, S. Barker, 1 ♂, Khanyinis Station, Minuma on *C. littoralis*, 26.1.1963, S. Barker.

23. *Astraeus (Astraeus) major* Blackburn, 1890: 1257, 1258; 1891: 496. Kerremans, 1892: 102; 1902: 149.

Astraeus navarchis var. *major*: Carter, 1929: 282. Obenberger, 1930: 366.

FIGS 17, 23C

Type. Holotype, BM (not seen by author).

Colour. Shiny. Head coppery with metallic reflections; antennae coppery-green or blue. Pronotum dark blue with purple reflections. Elytra dark blue with blue and purple reflections, each elytron with the following yellow markings: a fascia running from the shoulder transversely across the base towards the suture but not touching it; before the middle a thick fascia running from the margin transversely to the suture; after the middle there is a fascia commencing at the margin, running towards the suture but not reaching it. There is an oval red spot in the region of the marginal spine. The outer margins of the fascia and humeral fold are red. Undersurface dark blue with metallic purple reflections; hairs yellow. Legs red-brown; tarsi blue.

Shape and sculpture. Head with sparse shallow punctures at the base, wrinkled towards the apex; with a thin median keel; hairy. Pronotum with small shallow punctures in the middle, larger deeper ones at the sides with an irregular glabrous longitudinal area in the middle; there is a short median longitudinal impressed line projecting forwards from the basal crypt; short with the sides gradually rounded from base to apex. Elytra punctate-striate from the base for most of the length, the intervals between the striae convex, costate at the apex only; parallel-sided until just after the middle then gradually rounded to the marginal spine; both spines well developed; humeral fold poorly developed and slightly angled. Undersurface densely punctured at the sides, sparsely and shallowly punctured in the middle; hairy.

Size. Males $15.3 \pm 0.70 \times 5.9 \pm 0.22$ mm (4). Females $15.5 \pm 0.98 \times 6.3 \pm 0.91$ mm (2).

Distribution. Western Australia, South Australia and Victoria.

General remarks. I have no evidence of overlap in the distribution of this species, which

is found in low rainfall areas of three states, and *Astraeus navarchis*, which is presumably found in higher rainfall areas in Victoria. Because of differences in distribution and appearance I have treated the two as distinct species.

Specimens examined. W. Aust.: 1 ♂, WAM, 73-62; 1 ♂, Jung, SAM; 1 ♂, Wiaki on *Acacia coolgardiana*, 18.ix.1957, S. Barker, WAM, 73-60; 1 ♂, Culham, 6.ix.1961, R. P. McMillan, WAM, 73-61. S. Aust.: 1 ♀, Monarto, J. G. O. Tepper, SAM. Vic.: 1 ♀, Sea Lake, Goudie, NM.

24. *Astraeus (Astraeus) navarchis* (Thomson)

Conognatha navarchis Thomson, 1856: 115, 116, pl. 6, fig. 2. Masters, 1886: 79. *Astraeus navarchis*: Saunders, 1871: 43. van de Poll, 1886: 176. Masters, 1886: 71. van de Poll, 1889: 84, 91, 92, pl. 2, fig. 5, 5a. Blackburn, 1890: 1257. Kerremans, 1892: 102. Blackburn, 1892: 211. Kerremans, 1902: 148. Carter, 1929: 282. Obenberger, 1930: 366.

FIG. 23D

Type. Holotype, MNHN (not seen by author).

Colour. Shiny. Head coppery at the apex, dark blue and purple at the base; antennae dark brown, segments one and two with golden-green reflections, the rest with blue and purple reflections. Pronotum coppery at the apex and sides, dark blue and violet at the base. Elytra black with violet reflections; each elytron with two yellow fascia, the first commencing at the margin and covering the humeral fold, slightly concave towards the base and touching the suture, the second after the middle, commencing at the margin and running transversely towards the suture but not touching it. Undersurface: prothoracic sternites metallic golden-green, abdomen metallic violet; hairs yellow. Legs red-brown with violet reflections.

Shape and sculpture. Head closely punctured at the base, grooved and wrinkled at the apex; slightly excavated between the eyes towards the base, but with a thin glabrous median keel commencing anterior to this; hairy. Pronotum with small punctures in the middle, but mainly lacking in the centre, forming an indefinite median longitudinal glabrous line, the punctures larger and deeper at the sides; a median longitudinal impressed line projects forwards from the basal crypt to the middle; short, rounded at the sides and narrowed from base to apex. Elytra punctate-striate, the intervals convex at the base, flat at the apex, those in the centre with a shallow row of punctures, those at the sides with deep punctures;

parallel-sided until after the middle, then rounded and narrowed to the marginal spine; both spines well developed; humeral fold poorly developed and slightly angled. Undersurface: anteriorly the punctures are small in the middle and larger at the sides, on the abdomen uniformly small; hairy.

Size. Males $14.4 \pm 0.41 \times 5.5 \pm 0.13$ mm (7). Females $16.2 \pm 0.34 \times 6.6 \pm 0.08$ mm (5).

Distribution. Victoria.

General remarks. This species shows close affinity with *A. major*.

Specimens examined. Vic.: 2 ♂, SAM; 1 ♀, Jan Juc, NM; 5 ♂ & 4 ♀, NM.

25. *Astraeus (Astraeus) fraterculus* van de Poll, 1889: 84, 92, 93, pl. 2, figs 6, 6a. Kerremans, 1892: 102; 1902: 149, Carter, 1929: 282. Ohenberger, 1930: 365.

FIG. 23E

Type. Holotype MNHN (not seen by author).

Colour. Shiny. Head antennae and pronotum blue-black with blue reflections. Elytra blue-black, each elytron with two yellow fasciae; the first commencing at the shoulder and covering the humeral fold, then running transversely towards the suture but not touching it, concave towards the base; the second after the middle, commencing at the margin and running transversely towards the suture but not touching it. Undersurface deep metallic blue; hairs silver; Legs deep metallic blue.

Shape and sculpture. Head shallowly and sparsely punctured; with a small median keel; hairy. Pronotum sparsely but evenly punctured, the punctures at the sides larger and deeper than those in the middle; a short median longitudinal impressed line projects forwards from the basal crypt; short, the sides tapering acutely from base to apex, slightly rounded in the middle. Elytra costate, the intervals flat with irregular shallow punctures; parallel-sided until after the middle, then rounded and narrowed to the marginal spine; both spines well developed; humeral fold poorly developed and slightly angled. Undersurface with small shallow punctures in the middle, larger and deeper punctures at the sides; hairy.

Size. Males $9.3 \pm 0.30 \times 4.2 \pm 0.10$ mm (7). Females $8.8 \pm 0.30 \times 4.0 \pm 0.11$ mm (3).

Distribution. Western Australia.

General remarks. The external morphology of this species is very similar to that of *A. major*

and *A. navarchis*, however male genitalia is different (Fig. 23E). Therefore I do not group the three species together but place *A. fraterculus* next to *A. major* and *A. navarchis*.

Specimens examined. W. Aust.: 3 ♂ & 1 ♀, Borden on *Hakea trifurcata*, November 1939, H. W. Brown, WAM, 73-378/381; 1 ♀, Bushmead, 18.xi.1939, R. P. McMillan, WAM, 73-383; 2 ♂ & 1 ♀, Hopetoun, 18.x.1946, Mrs. Morris, WAM, 96-1910/1912; 1 ♂, Wembly on *Davlesia divaricata*, 5.ix.1970, S. Barker; 1 ♂, Borden, WAM, 73-382.

26. *Astraeus (Astraeus) prothoracicus* van de Poll, 1889: 85, 98, 99, pl. 3, fig. 11, 11a. Kerremans, 1892: 102; 1902: 149, Carter, 1929: 282. Ohenberger, 1930: 366.

FIG. 23F

Type. Holotype, MNHN (not seen by author).

Colour. Shiny. Head, antennae and pronotum bronze. Elytra dark brown with bronze reflections, each with the following yellow markings: along the margin there is a vitta, commencing at the shoulder and ending in the preapical area which may be broken into several elongate spots; in the middle but not touching the suture there is a vitta commencing on the anterior edge and ending in the preapical area, this is usually broken into a basal spot, a spot before the middle and an elongate spot after the middle. Undersurface bronze; hairs silver. Legs red-brown.

Shape and sculpture. Head closely and evenly punctured; no median keel; hairy. Pronotum with punctures wrinkled at the front and sides, projecting conically in the middle where the punctures coalesce and become strigose; gently rounded at the sides from the base to the middle, then tapered and narrowed to the apex, the apical edge broadly convex in the middle; hairy. Elytra costate, the intervals flat with a deep row of punctures; parallel-sided until after the middle then very gently rounded to the marginal spine; both spines poorly developed, blunt and close together; humeral fold poorly developed and slightly angled. Undersurface: punctures closer at the sides than in the middle; legs and whole undersurface densely covered with hair.

Size. Males $10.4 \pm 0.33 \times 3.7 \pm 0.13$ mm (3). Females $10.5 \pm 0.25 \times 3.9 \pm 0.17$ mm (6).

Distribution. Western Australia and Queensland.

General remarks. van de Poll (1889) listed the two specimens he had as coming from Clarence River and Champion Bay, and Car-

ter (1929) gave the range as Clarence River, N.S.W. It is now known that in Western Australia the species is associated with *Banksia prionotes* which occurs on yellow sandplain in a wide area between Shark Bay and Esperance. van de Poll's reference to Champion Bay would be to the Geraldton area. I have not located a specimen from N.S.W. Overall the body shape of this species is elongate and more or less cylindrical.

Specimens examined. Qld: 1 ♀, Myall Park, Glenmorgan, Nov. 1962, Dorothy Gordon, IH. W. Aust.: 2 ♂ & 1 ♀, Tammin, 21.xi.1939, A. M. Douglas, WAM, 39-2668/70; 1 ♂ & 3 ♀, Goomalling, 14.i.1950, R. P. McMillan, WAM, 73-371/374; 1 ♀, 19 km N of Northampton, 1.i.1972, K. T. Richards, WADA.

27. *Astraeus (Astraeus) elongatus* van de Poll, 1886: 177; 1889: 85, 101, 102, pl. 3, fig. 14, 14a, Kerremans, 1892: 101; 1902: 148, Carter, 1929: 282, Ohenberger, 1930: 365.

FIG. 23G

Type. Holotype, MNHN (not seen by author).
Colour. Shiny. *Male.* Head and pronotum green; antennae blue-green. Elytra black with purple-blue reflections; with the following yellow markings: a single spot at the base; a spot at the shoulder covering the humeral fold; a spot on the outer margin at the middle; a spot between the previously described one and the apex; near the suture but not touching it there is a large spot before the middle, a smaller one after the middle and a smaller pre-apical spot. Undersurface and legs green; hairs silver.

Female. Head and pronotum golden-green with golden reflections; antennae blue-green. Elytra as in the male. Undersurface and legs golden-green; hairs silver.

Shape and sculpture. Head deeply and evenly punctured; no median keel; hairy. Pronotum with punctures closer at the sides than in the middle; with a short median longitudinal impressed line projecting forwards from the basal crypt; laterally dilated and with the apical edge projecting in the middle; hairy. Elytra punctate-striate at the base costate towards the apex, the intervals flat and slightly transversely wrinkled; more or less parallel-sided, rounded after the middle to the marginal spine; both spines well developed; humeral fold poorly developed, slightly angled. Undersurface closely punctured; hairy.

Size. Males $10.5 \pm 0.4 \times 3.7 \pm 0.13$ mm (8).

Females $11.8 \pm 0.28 \times 4.2 \pm 0.11$ mm (12).

Distribution. Western Australia.

General remarks. A single specimen collected at Dryandra has a bright blue head and prothorax. Overall the body shape is elongate and cylindrical. This species has closest affinity with *A. prothoracicus*.

Specimens examined. W. Aust.: 7 ♂ & 9 ♀, Quairading on *Xanthorrhoea* sp., 19.x.1970, S. Barker; 1 ♂ & 2 ♀, Quairading on *Xanthorrhoea*, 7.xi.1970, S. Barker; 1 ♀, Dryandra on *Casuarina hurgellana*, 8.xii.1970, S. Barker.

28. *Astraeus (Astraeus) vittatus* van de Poll, 1889: 85, 99, 100, pl. 3, fig. 12, 12a. Kerremans, 1892: 102, Carter, 1929: 282, Ohenberger, 1930: 367.

Astraeus vittatus. Kerremans, 1902: 149.

FIG. 23H

Type. Holotype, MNHN (not seen by author).

Colour. Shiny. Head and pronotum black with purple reflections; antennae black with blue reflections, the apex on the first, second and third segments dark brown with purple reflections. Elytra black with violet reflections, each with the following yellow markings: a vitta along the margin from the shoulder to the preapical region, broken just after the middle; a vitta in the middle but not touching the suture from the base to near the apex, broken near the middle. Undersurface metallic purple; hairs silver. Legs brown.

Shape and sculpture. Head broad and closely punctured; no median keel; hairy. Pronotum with small and shallow punctures in the middle, larger and deeper at the sides; gradually rounded from base to apex; the anterior margin projecting forwards in the middle, hairy. Elytra punctate-striate at the base, faintly costate at the apex and slightly wrinkled, the intervals slightly convex at the base and flat at the apex, each with a row of punctures; parallel-sided until just after the middle, then tapered to the very short marginal spine, sutural spine very broad, humeral fold poorly developed, slightly angled. Undersurface closely and densely covered with fine punctures; hairy.

Size. Male 9.9×3.7 mm (1).

Distribution. Western Australia.

Specimens examined. W. Aust.: 1 ♂, Watling, 10.xii.1950, R. P. McMillan, WAM, 71-1761.

29. *Astraeus (Astraeus) flavopictus* LaPorte & Gory, 1837: 2, pl. 1, fig. 1. Imhoff, 1856: 46, Lacordaire, 1857: 43, Gemminger & de Harold, 1869: 1380, Masters, 1871:

124. Saunders, 1871: 43. Kerremans, 1885: 136. van de Poll, 1886: 176, 177. Masters, 1886: 71. van de Poll, 1889: 85, 97, 98, pl. 2, fig. 10, 10a. Kerremans, 1892: 101; 1902: 148. Carter, 1929: 282. Obenberger, 1930: 365. Barker, 1964: 306, 307.

FIG. 231

Type. Holotype, MNHN (not seen by author).

Colour. Shiny. Head and pronotum brown with variable green and/or purple reflections; antennae black with blue reflections. Elytra brown with variable bronze and violet reflections, with the following yellow markings in two rows, one in the middle but not touching the suture, the other along the margin; in the middle; an elongate basal spot; a transverse bar before the middle; an elongate spot after the middle; a long thin preapical mark. Along the margin; an elongate spot from the shoulder covering the humeral fold; a spot in the middle; a spot after the middle. The three spots along the margin may coalesce forming a single vitta or be separated into two or three spots. Undersurface and legs bronze; hairs silver.

Shape and sculpture. Head densely punctured; no median keel; hairy. Pronotum closely and evenly punctured; basal half parallel-sided, thereafter rounded to the apex; apical edge projecting forward in the middle; a short impressed line projects forwards from the basal crypt; hairy. Elytra costate, the intervals flat but deeply punctured and slightly wrinkled; parallel-sided from base until after the middle, then narrowed to the small marginal spine; sutural spine short; humeral fold moderately developed and angled. Undersurface closely and evenly punctured; densely hairy as are the legs.

Size. Males $10.9 \pm 0.38 \times 3.9 \pm 0.17$ mm (12). Females $12.0 \pm 0.27 \times 4.4 \pm 0.10$ mm (15).

Distribution. Western Australia.

General remarks. This species shows closest affinity with *A. vittatus*.

Specimens examined. W. Aust.: 1 ♀, Porongroup, 28.ii.1963, F. H. Uther Baker; 1 ♂ & 1 ♀, 64 km along main York Rd, on *Jacksonia* sp., 1.i.1968, S. Barker; 11 ♂ & 13 ♀, 64 km along main York Rd, on *Jacksonia* sp., 6.xi.1970, S. Barker.

30. *Astraeus* (*Astraeus*) *macmillani* sp. nov.

FIGS 13, 231

Types.

Holotype: ♂, 77 km along main York Rd, W. Aust. on *Casuarina huegeliana*, 21.x.1970, S. Barker, SAM, 1.20955.

Allotype: ♀, 77 km along main York Rd, W. Aust. on *C. huegeliana*, 5.i.1968, S. Barker, SAM, 1.20956.

Paratypes: 1 ♂ & 1 ♀, 77 km along main York Rd, W. Aust. on *Casuarina* sp., 1.i.1968, S. Barker, EA; 2 ♂ & 2 ♀, 77 km along main York Rd, W. Aust. on *C. huegeliana*, 21.xi.1970, S. Barker, ANIC (1 ♂ & 1 ♀), BM (1 ♂), MNHN (1 ♀); 1 ♀, 77 km along main York Rd, W. Aust. on *C. huegeliana*, 5.i.1968, S. Barker, BM; 6 ♂ & 2 ♀, 77 km along main York Rd, W. Aust. on *C. huegeliana*, 7.xi.1970, S. Barker, MNHN (1 ♂), SAM (4 ♂ & 2 ♀), WAM (1 ♂); 1 ♂ & 2 ♀, 11 km S of Walebing, W. Aust., 6.x.1971, K. T. Richards, WADA; 1 ♀, 77 km along main York Rd, W. Aust. on *C. huegeliana*, 5.i.1968, S. Barker, WAM.

Colour. Shiny. Head black with purple reflections; antennae black with metallic blue reflections, each of segments 1-4 with dark brown apex. Pronotum black with blue-green reflections in the middle, purple reflections in the front and at the sides. Elytra black with purple reflections, each with the following yellow markings: a large spot at the base; a fascia commencing at the shoulder, covering the humeral fold and running transversely towards the suture but not touching it, concave towards the base (sometimes broken into a marginal and a medial spot); a small spot after the middle on the outer margin; an oval preapical spot; between the last two spots a short fascia, running from the margin, half way to the suture. Undersurface metallic purple and bronze; hairs silver. Legs red-brown.

Shape and sculpture. Head closely punctured; no median keel; hairy. Pronotum deeply and closely punctured at the sides, sparsely in the middle; a median longitudinal impressed line projects forwards from the basal crypt to the middle; parallel-sided at the base then rounded and narrowed to the apex. Elytra costate, the intervals flat each with a shallow row of punctures; more or less parallel-sided until the middle then rounded and tapered to the marginal spine; both spines well developed; humeral fold moderately developed and angled. Undersurface: thoracic sternites finely and sparsely punctured in the middle more closely at the sides; abdominal segments finely and closely punctured; hairy.

Size. Males $10.5 \pm 0.10 \times 3.9 \pm 0.04$ mm (47). Females $11.7 \pm 0.15 \times 4.3 \pm 0.06$ mm (36).

Distribution. Western Australia.

General remarks. In some species the marginal spot is reduced or lost, in others there is an additional spot close to the suture and between the two fascia. Named after Mr R. P. McMillan.

Specimens examined. W. Aust.: Types: 5 ♂ & 4 ♀, 77 km along main York Rd on *Casuarina* sp., 5.i.1968, S. Barker; 11 ♂, Dryandra on *Casuarina* sp., 21.x.1970, S. Barker; 6 ♂ & 6 ♀, Dryandra on *Casuarina huegeliana*, 11.xi.1970, S. Barker; 2 ♂ & 2 ♀, 6 km E of North Hannister on *C. huegeliana*, 19.xi.1970, S. Barker; 6 ♂ & 4 ♀, 77 km along main York Rd on *C. huegeliana*, 21.xi.1970, S. Barker; 1 ♂ & 3 ♀, 77 km along main York Rd on *C. huegeliana*, 7.xii.1970, S. Barker; 5 ♂ & 7 ♀, Dryandra on *C. huegeliana*, 8.xii.1970, S. Barker; 1 ♂, Dryandra on *C. huegeliana*, 12.i.1973, S. Barker.

31. *Astraeus (Astraeus) carnabyi* sp. nov.

FIGS 1d, 14, 23K

Types.

Holotype: ♂, 16 km NE of Lake Grace, W. Aust., on *Casuarina huegeliana*, 9.i.1972, E. & K. Carnaby, SAM, 120947.

Allotype: ♀, 16 km NE of Lake Grace, W. Aust., on *C. huegeliana*, 3.i.1971, E. & K. Carnaby, SAM, 120948.

Paratypes: 1 ♂ & 1 ♀, 16 km NE of Lake Grace, W. Aust., on *C. huegeliana*, 9.i.1972, E. & K. Carnaby, ANIC; 1 ♀, 16 km NE of Lake Grace, W. Aust., on *C. huegeliana*, 25.i.1973, E. & K. Carnaby, BM; 1 ♂ & 1 ♀, 16 km NE of Lake Grace, W. Aust., on *C. huegeliana*, E. & K. Carnaby, KC; 1 ♂ & 1 ♀, 16 km NE of Lake Grace, W. Aust., on *C. huegeliana*, 25.i.1972, E. & K. Carnaby, MNHN (1 ♂), WAM (1 ♀); 1 ♀, 24 km S of Lake King, W. Aust., on *C. huegeliana*, 25.i.1973, S. Barker, MNHN; 4 ♂ & 1 ♀, 14 km N of Needilup, W. Aust., on *C. huegeliana*, 14.xii.1972, K. T. Richards, WADA.

Colour. Shiny. Head, pronotum and elytra black with purple reflections; antennae black with blue and purple reflections. Each elytron with the following yellow markings: an elongate spot at the base reaching the anterior margin; a fascia commencing at the anterior lateral margin, covering the humeral fold then running upwards towards the suture but not touching it, concave forwards; a small fascia just after the middle, commencing at the margin and at right angles to the suture but reaching only half way to it; midway between the two fascia are two small spots, one on the margin and the other near the suture but not touching it; a small preapical spot. Undersurface metallic purple; hairs silver. Legs dark, upper sides with metallic blue reflections, undersides metallic purple.

Shape and sculpture. Head with medium sized punctures on basal half merging into irregular

longitudinal channels on apical part; no median keel; hairy. Pronotum evenly punctured, with a median glabrous line at the base and apex; sides rounded gradually from base to apex; hairy. Elytra costate, the intervals between flat, each with a row of shallow punctures; parallel-sided until just after the middle, then rounded off to the strong marginal spine; well developed sutural spine; humeral fold poorly developed but slightly angled. Undersurface evenly and shallowly punctured; hairy. *Size.* Males $9.8 \pm 0.17 \times 3.7 \pm 0.06$ mm (8). Females $10.6 \pm 0.23 \times 4.0 \pm 0.11$ mm (7).

Distribution. Western Australia.

General remarks. Named after Mr K. Carnaby.

Specimens examined. Types only.

32. *Astraeus (Astraeus) budeni* van de Poll, 1889: 84, 93, 94, pl. 2, fig. 7, 7a. Blackburn, 1891: 496. Kerremans, 1892: 101. van de Poll, 1892: 67. Blackburn, 1895: 45, 46. Kerremans, 1902: 148. Carter, 1929: 282. Obenberger, 1930: 365.

Astraeus budeni var. *disjunctus* Obenberger, 1928: 204; 1930: 365.

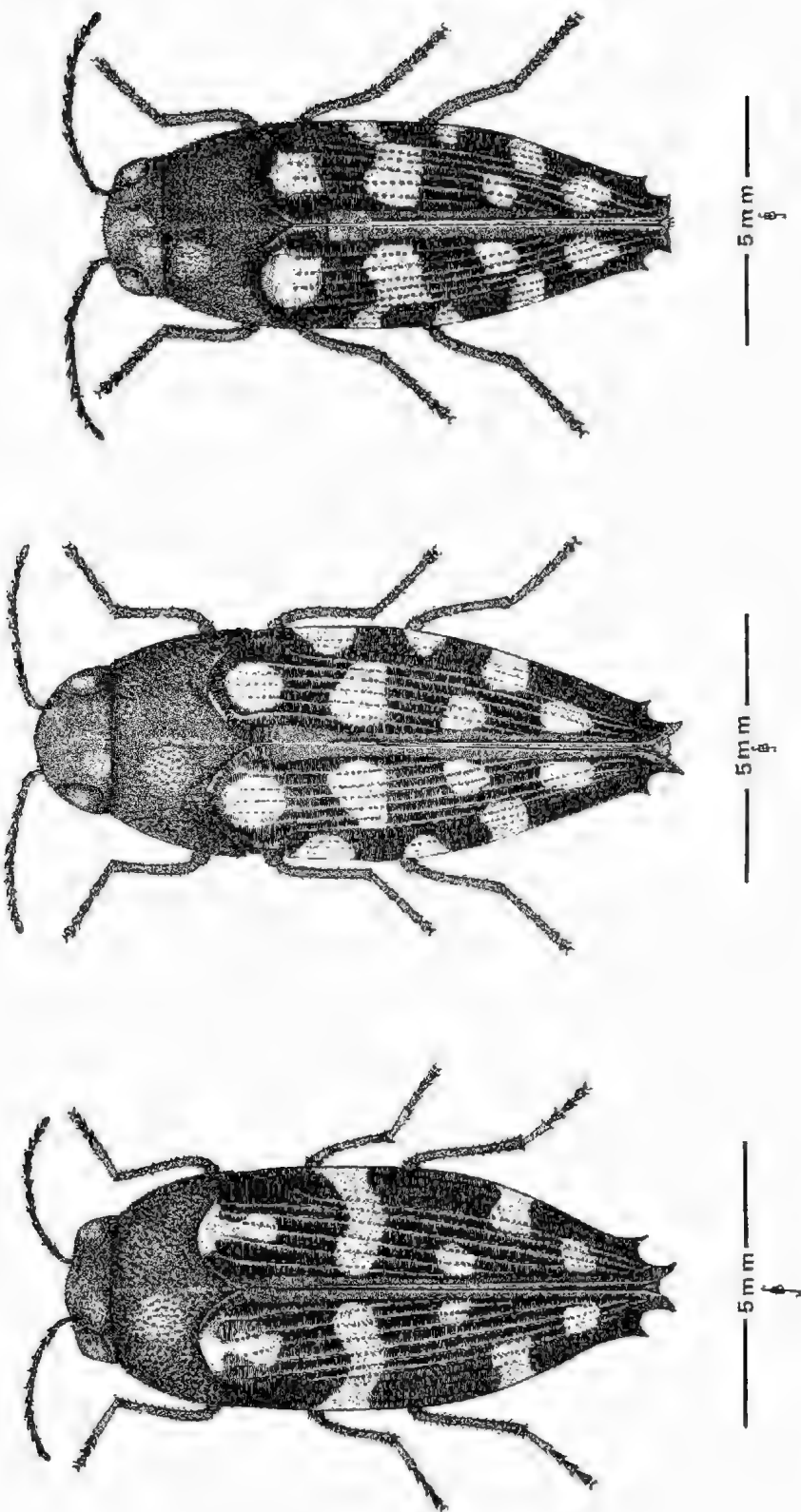
Astraeus meyricki Blackburn, 1890: 1256, 1257. Kerremans, 1892: 102. Blackburn, 1895: 45, 46.

FIG. 23L

Type. *Holotype:* ♀ MNHN (seen by author).

Colour. Shiny. Head, pronotum and elytra black with blue reflections; antennae black with blue reflections, tips of first and second segments brown. Elytra: each elytron with the following yellow markings: a spot at the base; a fascia commencing at the margin on the humeral fold, running obliquely upwards and backwards and then at right angles to the longitudinal axis of the body, just before the middle and not touching the suture (this is frequently broken to form two spots *vide* var. *disjunctus* Obenberger, but this has no taxonomic significance); just after the middle there is a small fascia commencing at the margin, slightly concave to the apex and not touching the suture. Undersurface and legs dark with metallic purple reflections; hairs silver.

Shape and sculpture. Head evenly punctured; no median keel; hairy. Pronotum with shallow punctures larger at the sides than in the middle; at the sides gradually rounded and narrowed from base to apex; hairy. Elytra costate, the intervals between flat each with a row of shallow punctures; parallel-sided until after the middle then rounded off to the marginal spine; strong sutural spine; humeral fold

Fig. 14. *Astraeus carabyi* sp. nov.Fig. 15. *Astraeus carteri* sp. nov.Fig. 16. *Astraeus goerlingi* sp. nov.

poorly developed but slightly angled. Undersurface, punctures sparser in the middle than at the sides; hairy.

Size. Males $8.8 \pm 0.14 \times 3.4 \pm 0.07$ mm (16). Females $8.9 \pm 0.16 \times 3.5 \pm 0.07$ mm (17).

Distribution. All of mainland Australia except the Northern Territory.

General remarks. This species was described almost simultaneously by van de Poll as *A. badeni* and by Blackburn as *A. meyricki*. Blackburn (1891) recognised *A. meyricki* as a synonym of *A. badeni*, but later changed his mind and called *A. meyricki* a good species (Blackburn 1895). Distance between the two populations was the main argument used by Blackburn (1895) in favour of calling the eastern and western representatives two distinct species. I have been unable to separate specimens collected in Western Australia from those collected in South Australia.

Specimens examined. *S. Aust.*: Type; 1 ♂ & 1 ♀, Morgan, *A. M. Lea*, SAM; 1 ♀, Murray Bridge, Oct. 1911, SAM; 8 ♂ & 6 ♀, on *Melaleuca* sp., Derna Pass (probably the same as Puttapa Gap), 21 km S of Copley, 25.x.1969, *N. McFarland*, SAM; 7 ♂ & 9 ♀, Puttapa Gap, Flinders Ranges on *Melaleuca glomerata*, 21.x.1971, *S. Barker*, *W. Aust.*: Paratype of *A. meyricki* Blackburn, SAM; 1 ♀, 18 km SW of Three Springs on *Dryandra cirsoides*, 8.x.1968, *N. McFarland*, SAM; 3 ♂ & 3 ♀, Iuranda rockhole, 106 km S of Balladonia on *Callitris preissii*, 9.xii.1974, *S. Barker*, *N.S.W.*: 1 ♀, *W. du Boulay*, WAM, 73-54. *Qld.*: Type ♀ *A. badeni* var. *disjunctus* Obenberger, NMP, 21 990.

33, *Astraeus (Astraeus) jansoni* van de Poll, 1889: 84, 94, 95, pl. 2, fig. 8, 8a; Blackburn, 1891: 496, Kerremans, 1892: 102, van de Poll, 1892: 68, Blackburn, 1894: 101; 1895: 46, Kerremans, 1902: 148, Carter, 1929: 282, Obenberger, 1930: 366, Carter, 1933: 42.

Astraeus tepperi Blackburn, 1890: 1258, 1259

FIG. 23M

Type. Holotype, MNHN (not seen by author).

Colour. Shiny. Head, pronotum and elytra bronze-green or black with green or purple reflections; antennae black with blue or purple reflections. Elytra: each elytron with the following yellow markings; along the margin, a spot at the shoulder half covering the humeral fold, a spot before the middle, a fascia after the middle running transversely towards the suture but not touching it; in the middle near the suture but not touching it, a spot at the base, a spot before the middle, a spot at the

middle, a preapical spot. Undersurface and legs metallic bronze-green; hairs silver.

Shape and sculpture. Head evenly punctured, slightly excavated in the middle between the eyes; no median keel; hairy. Pronotum evenly punctured; a short longitudinal median impressed line projects forwards from the basal crypt; at the sides rounded basally, then tapered and narrowed to the apex; hairy. Elytra costate, the intervals between flat, each with a deep row of punctures and faintly transversely wrinkled; parallel-sided until after the middle, then rounded and narrowed to the marginal spine; both spines well developed; humeral fold poorly developed and slightly angled. Undersurface with small shallow punctures in the middle, larger and deeper at the sides; hairy.

Size. Males $8.1 \pm 0.08 \times 3.2 \pm 0.04$ mm (37). Females $8.6 \pm 0.15 \times 3.4 \pm 0.06$ mm (32).

Distribution. Mainland eastern Australia from South Australia to Queensland.

General remarks. The yellow pattern is variable; there are either six spots and a fascia on each elytron or the fascia may be broken in the middle giving a total of eight spots.

Specimens examined. *S. Aust.*: 2 ♀, McDonald Ferris N.P. on *Callitris preissii*, 2.xi.1967, *S. Barker*; 1 ♂ & 1 ♀, 2 km E of Hartley on *C. preissii*, 15.xi.1969, *S. Barker*; 7 ♂ & 7 ♀, McDonald Ferris N.P. on *C. preissii*, 15.xi.1969, *S. Barker*; 2 ♂ & 2 ♀, on road N of Parra Wirra N.P. on *C. preissii*, 10.xii.1969, *S. Barker*; 7 ♂ & 11 ♀, Tothill Ranges near Brady Creek on *C. preissii*, 12.xii.1969, *S. Barker*; 1 ♀, Onkaparinga Gorge near Hackham on *Callitris rhomboides*, 27.xii.1969, *S. Barker*; 11 ♂ & 5 ♀, Mt Remarkable N.P. on *C. preissii*, 30.xii.1969, *S. Barker*; 2 ♂ & 2 ♀, Alligator Gorge N.P. on *C. preissii*, 30.xii.1969, *S. Barker*; 5 ♂ & 2 ♀, Mt Remarkable N.P. on *C. preissii*, 22.x.1971, *S. Barker*; 1 ♂, McDonald Ferris N.P. on *C. preissii*, 14.xi.1971, *S. Barker*; 2 ♂, 16 km N of Mannum on *C. preissii*, 20.xi.1971, *S. Barker*; 6 ♂ & 7 ♀, Salter Springs on *C. preissii*, 24.ix.1972, *S. Barker*; 4 ♂ & 3 ♀, Alligator Gorge N.P. on *C. preissii*, 8.x.1972, *S. Barker*; 1 ♂, 10 km W of Penneshaw, Kangaroo I. on *C. preissii*, 24.xi.1972, *S. Barker*; 1 ♂ & 1 ♀, near Rocky Point, Kangaroo I. on *C. preissii*, 21.x.1974, *S. Barker*. *Qld.*: 7 ♀, Stanthorpe, *E. Sutton*, QM

34, *Astraeus (Astraeus) oberthuri* van de Poll, 1889: 85, 100, 101, pl. 3, fig. 13, 13a. Kerremans, 1892: 102, Blackburn, 1892: 211, Kerremans, 1902: 149, Carter, 1929: 282, Obenberger, 1930: 366.

FIG. 23N

Type. Holotype ♂, MNHN (seen by author).

Colour. Shiny. Head, antennae and pronotum

black with purple and blue reflections; Elytra black with purple reflections, each with the following yellow markings: a basal spot; a fascia commencing at the shoulder, covering the humeral fold and running towards the suture but not touching it, slightly concave towards the base; a spot at the middle touching the margin; a preapical spot; a spot midway between the previous two which may or may not touch the margin; a spot midway between the fascia and the preapical spot, near the suture but not touching it, absent in some specimens. Undersurface and legs metallic purple; hairs silver.

Shape and sculpture. Head closely and evenly punctured at the base and sides, punctures coalescing and wrinkled at the apex; no median keel; hairy. Pronotum closely and evenly punctured in the middle, punctures coalescing and wrinkled at the sides; a short median longitudinal impressed line projects forwards from the basal crypt; parallel-sided from the base until after the middle, then rounded and narrowed to the apex, front edge projecting slightly in the middle; dorsally convex in lateral profile; hairy. Elytra costate, the intervals between flat, each with a row of punctures and faintly transversely strigose; parallel-sided to the middle then rounded and tapered to the small marginal spine; sutural spine well developed; humeral fold poorly developed and slightly angled. Undersurface with shallow punctures closer at the sides than in the middle; hairy.

Size. Males $9.7 \pm 0.10 \times 3.6 \pm 0.04$ mm (58). Females $9.8 \pm 0.34 \times 3.6 \pm 0.15$ mm (18).

Distribution. Western Australia.

Specimens examined. W. Aust.: Type; 1 ♂, Yanchep, 7.i.1962, F. H. Utter Baker; 3 ♀, Gosnells on *Casuarina* sp., 7.i.1967, S. Barker; 19 ♂ & 1 ♀, 8 km W of Beverly, 1.O. from Brookton Rd, on *Casuarina* sp., 1.i.1967, S. Barker; 1 ♂, 77 km along main York Rd, on *Casuarina* sp., 1.i.1968, S. Barker; 8 ♂ & 1 ♀, Red Hill Rd, near Midland Junction on *Casuarina* sp., 4.i.1968, S. Barker; 2 ♂, 77 km along main York Rd, on *Casuarina* sp., 5.i.1968, S. Barker; 6 ♂ & 2 ♀, 77 km along main York Rd, on *Casuarina huegeliana*, 7.xi.1970, S. Barker; 3 ♂ & 2 ♀, 7 km E of North Bannister on *C. huegeliana*, 19.xi.1970, S. Barker; 8 ♂ & 3 ♀, 13 km E of North Bannister on *C. huegeliana*, 19.xi.1970, S. Barker; 5 ♂ & 3 ♀, 77 km along main York Rd, on *C. huegeliana*, 21.xi.1970, S. Barker; 1 ♂, 77 km along main York Rd, on *C. huegeliana*, 7.xii.1970, S. Barker; 3 ♂ & 2 ♀, Wannamal on *C. huegeliana*, 10.xii.1970, S. Barker; 2 ♂, 135 km along Albany Highway on *C. huegeliana*, 10.i.1973, S. Barker.

35. *Astraeus (Astraeus) watsoni* sp. nov.

FIG. 13

Types.

Holotype: ♀, Borden, W. Aust., 16.xii.1957, R. P. McMillan & J. A. L. Watson, WAM, 71-1761.

Paratypes: 1 ♀, ANIC; 1 ♀, Goomalling, W. Aust., SAM; 1 ♀, W. Aust., SAM; 1 ♀, Borden, W. Aust., 16.xii.1957, R. P. McMillan & J. A. L. Watson, MNHN; 1 ♀, Borden, W. Aust., 16.xii.1957, R. P. McMillan & J. A. L. Watson, WAM, 71-1760.

Colour. Shiny. Head, pronotum and elytra black with blue and purple reflections; antennae black with blue and purple reflections, the base and apex of the first segment and apex of the second segment brown. Elytra; each elytron with the following yellow markings: a large basal spot; a broad fascia commencing at the margin and covering the humeral fold, running transversely towards the suture but broken in the middle forming a large spot near the suture but not touching it; after the middle, a broad fascia concave backwards and not touching the margin or the suture; a small preapical spot; a small spot between the fascia near the margin but not touching it. Undersurface black with blue and purple reflections; hairs silver. Legs brown; top edges of the femur and top surfaces of the tarsi dark brown.

Shape and sculpture. Head shallowly but evenly punctured; with a median keel; covered with very long hair. Pronotum with punctures evenly dispersed; a median longitudinal impressed line projects forwards from the basal crypt to the middle; sides gently rounded and narrowed from base to apex; hairy. Elytra costate, the intervals between convex at the basal half, flat at the apical half, each with a row of shallow punctures and slightly transversely wrinkled; parallel-sided until just before the middle, tapered gradually to the marginal spine which is moderately developed; strongly developed sutural spine; humeral fold moderately developed and angled. Undersurface evenly and shallowly punctured; hairy.

Size. Females $12.9 \pm 0.73 \times 4.6 \pm 0.30$ mm (6).

General remarks. Named after Dr J. A. L. Watson.

Specimens examined. Types only.

36. *Astraeus (Astraeus) carteri* sp. nov.

FIGS 15, 230

Types.

Holotype: ♂, 383 km along Payne's Find Rd, W. Aust., on *Casuarina dielsiana*, 17.ix.1970, S. Barker, SAM, I 20949.

Allotype: ♀, Lake King, W. Aust., 18.xii.1970, E. & K. Carnaby, SAM, T 20950.

Paratypes: 3 ♂, 383 km along Payne's Find Rd, W. Aust., on *C. dielsiana*, 17.ix.1970, S. Barker, ANIC (1 ♂), BM (1 ♂), MNHN (1 ♂); 3 ♂ & 1 ♀, Borden, W. Aust., on *Casuarina glauca*, 16.x.1939, H. W. Brown, ANIC (1 ♀), WAM (3 ♂), WAM, 73-68/70; 2 ♀, Lake Grace, W. Aust., MNHN (1 ♀), WAM (1 ♀), WAM, 73-66; 3 ♂, Lake Grace, H. W. Brown, WAM, 33-735/6, 73-65; 1 ♂ & 1 ♀, Southern Cross, H. W. Brown, WAM, 73-67, 73-63; 2 ♂, Tallering Station, Pindar on *Casuarina* sp., 22.ix.1958, S. Barker, WAM, 73-72/3.

Colour. Shiny. Head black with purple reflections; antennae black with blue-green and purple reflections. Pronotum black with blue-green reflections on top and purple reflections at the margins. Elytra black with purple reflections with the following yellow markings: a spot at the base; a spot originating at the shoulder covering the humeral fold; a spot above the middle touching the outer margin; a spot below the middle, near the outer margin but not touching it; three spots close to the suture but not touching it, the first the largest above the middle, the next smaller below the middle and a longitudinally elongate preapical spot (the first of these sometimes coalesces with the spot covering the humeral fold to form a fascia, concave towards the base). Undersurface and legs dark metallic purple; hairs silver.

Shape and sculpture. Head closely punctured; no median keel; hairy. Pronotum evenly punctured; with a short median longitudinal impressed line projecting forwards from the basal crypt, running forwards from the impressed line is a glabrous line formed by lack of perforations, better defined in females where it reaches the anterior margin than in males where it runs only to the middle; sides rounded and narrowed to the strong marginal apex; dorsally flattened in lateral profile; hairy at the sides but less so in the middle. Elytra costate, the intervals between flat with a row of shallow punctures; sides at first diverging slightly outwards from the base then parallel-sided to before the middle, then gradually rounded and narrowed to the strong marginal spines; well developed sutural spines; humeral fold poorly developed but slightly angled. Undersurface finely and sparsely punctured in the middle more closely at the sides; densely hairy.

Size. Males $11.2 \pm 0.16 \times 4.0 \pm 0.08$ mm

(13). Females $12.0 \pm 0.92 \times 4.3 \pm 0.40$ mm (3).

Distribution. Western Australia.

General remarks. *A. carteri* shows closest affinity with the following group of species: *A. macmillani*, *A. carnabyi*, *A. hadeni*, *A. jansoni*, *A. oberthuri* and *A. watsoni*. Named after the late Mr H. J. Carter.

Specimens examined. Types only.

37: *Astracus (Astraeus) goerlingi* sp. nov.

FIGS 16, 23P

Types.

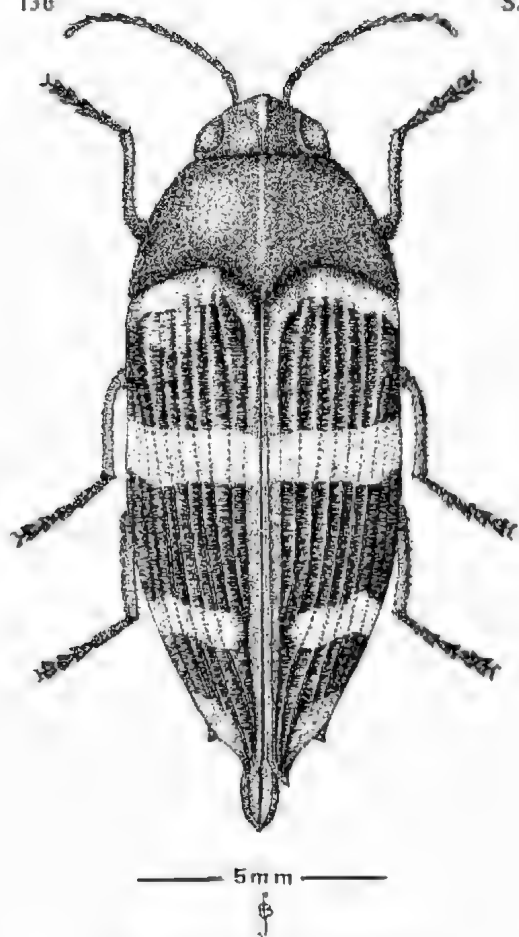
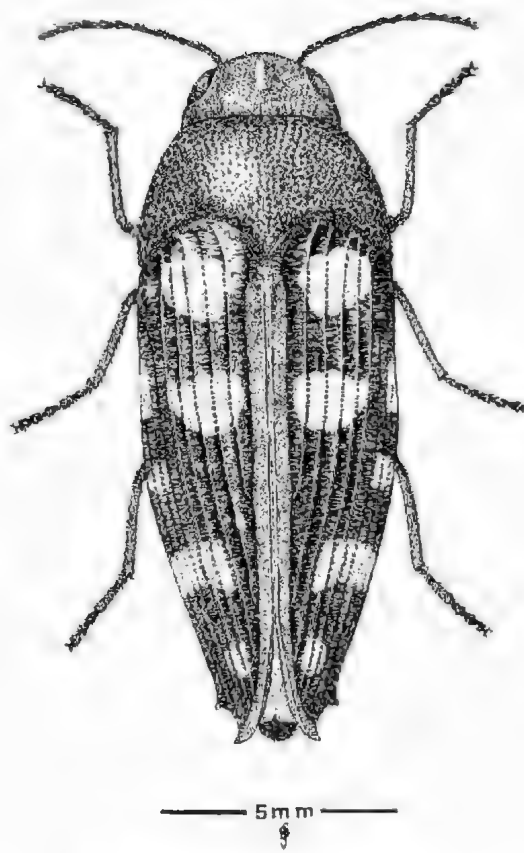
Holotype: ♂, Marloo Stn, Wurarga, W. Aust. 1931-1941, *A. Goerling*, ANIC.

Allotype: ♀, Marloo Stn, Wurarga, W. Aust. 1931-1941, *A. Goerling*, ANIC.

Paratypes: 4 ♂ & 3 ♀, Marloo Stn, Wurarga, W. Aust., 1931-1941, *A. Goerling*, ANIC (1 ♂ & 1 ♀), BM (1 ♂ & 1 ♀), SAM (1 ♂), WAM (1 ♂ & 1 ♀); 3 ♀, 106 km S of Payne's Find, W. Aust., on *Casuarina acutivalvis*, 18.ix.1970, S. Barker, SAM; 2 ♂ & 1 ♀, Wurarga, W. Aust. on *Casuarina principiana* 16.ix.1935, H. W. Brown, NM.

Colour. Shiny. Head, antennae and pronotum black with bronze, blue or purple reflections, or a combination of these colours. Elytra black with purple reflections, each with the following yellow markings: a basal spot; a fascia commencing at the shoulder and covering the humeral fold, running towards the suture but not touching it, concave towards the base; a spot at the middle touching the margin; a preapical spot; a spot midway between the two previously mentioned marks, elongate and touching the margin; a spot near the suture, but not touching it, midway between the fascia and the preapical spot. Undersurface and legs purple, coppery and bronze; hairs silver.

Shape and sculpture. Head closely and evenly punctured; slightly excavated in the middle between the bases of the eyes; no median keel; hairy. Pronotum with punctures larger at the sides than in the middle, median longitudinal glabrous line from base to apex formed by the absence of punctures; gently rounded at the sides from base to apex; hairy. Elytra costate at the apex, punctate-striate at the base, the intervals between flat at the apex and convex at the base, each with a row of punctures; parallel-sided to the middle then rounded and narrowed to the marginal spine, which is well developed; sutural spine sharp but shortened by the sutural margin being straight and superficially appearing to be broken; humeral fold poorly developed and slightly angled. Undersurface evenly punctured, the punctures

Fig. 17. *Astraeus major* BlackburnFig. 18. *Astraeus watsoni* sp. nov.

deeper at the sides than in the middle; hairy. In the male the last abdominal sternite has a marginal indentation in the centre.

Size. Males $10.8 \pm 0.12 \times 3.8 \pm 0.05$ mm (26). Females $11.7 \pm 0.19 \times 4.2 \pm 0.07$ mm (22).

Distribution. Western Australia.

General remarks. *A. goerlingi* shows features in common with the preceding group of species (Fig. 23P) and also with the following group of two species, and because of this I place it by itself between the two groups. Named after the late Mr A. Goerling.

Specimens examined. W. Aust.: Types; 20 ♂ & 14 ♀, Marloo Stn, Wurtarga, 1931-1941, A. Goerling, ANIC.

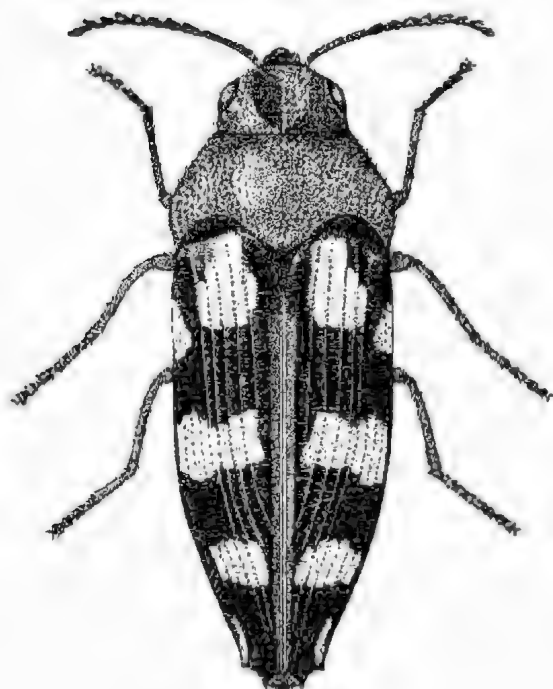
38. *Astraeus (Astraeus) cyaneus* Kerremans, 1900: 295; 1902: 148. Carter, 1929: 282. Obenberger, 1930: 365.

FIG. 19

Type. Holotype: ♂, Standing, N.S.W., DM (seen by author).

Colour. Shiny. Head and pronotum blue-green; antennae black with blue reflections. Elytra black with blue-green reflections, each with the following yellow markings: a large elongate basal spot not reaching the anterior margin or suture; a fascia at the middle, expanded towards the apex near the lateral margin but not touching it or the suture; a large spot after the middle, not touching the margin or the suture; a spot covering the humeral fold; a small elongate spot in the form of a lunette near the preapical margin and ending at the marginal spine (present in the illustrated specimen; absent in the holotype). Undersurface blue-green; hairs silver. Legs metallic blue.

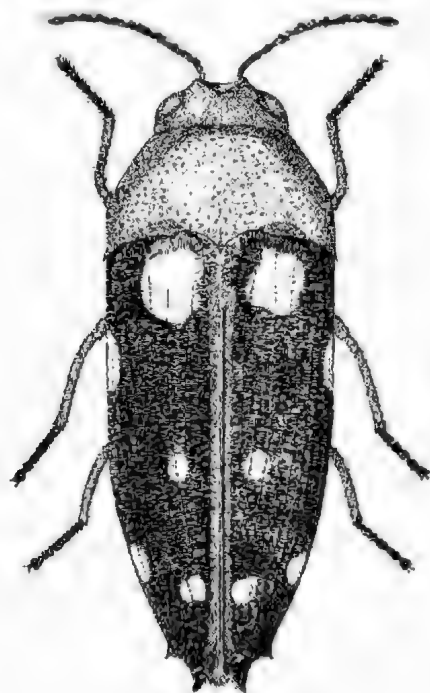
Shape and sculpture. Head evenly punctured; deeply excavated between the eyes, mainly at the base; no median keel; sparsely covered with long, fine hair. Antennae strongly serrate. Pronotum deeply punctured at the sides; towards the middle shallow punctures with a central ovoid area consisting of hexagonal

Fig. 19. *Astraeus cyaneus* Kerremans

depressions, each with a small central puncture; inflated at the sides just before the middle, then straight sided and strongly tapered to the apex; the lateral lobes with their apices turned downwards; convex at the apex, flattened at the base; covered with fine hair. Elytra flattened; punctate-striate anteriorly, costate posteriorly, the intervals between convex towards the base and flat at the apex, each with a single longitudinal row of shallow punctures and slightly transversely wrinkled; parallel-sided to the middle, then rounded and narrowed to the small marginal spine; sutural spine shortened by the sutural margin being straight and turned slightly upwards; humeral fold poorly developed but slightly angled. Undersurface evenly but shallowly punctured in the middle; lateral prosternum and abdominal sternites longitudinally grooved; sparsely haired.

Size. Males 11.6 x 3.9 mm (1). Females 13.9 x 4.8 mm (1).

Distribution. New South Wales and Queensland.

Fig. 20. *Astraeus caledonicus* Fauvel

Specimens examined. N.S.W.: Type. Old: 1 ♀, Acacia Creek via Killarnay, Jan. 1948, Mrs J. Harstett, JH.

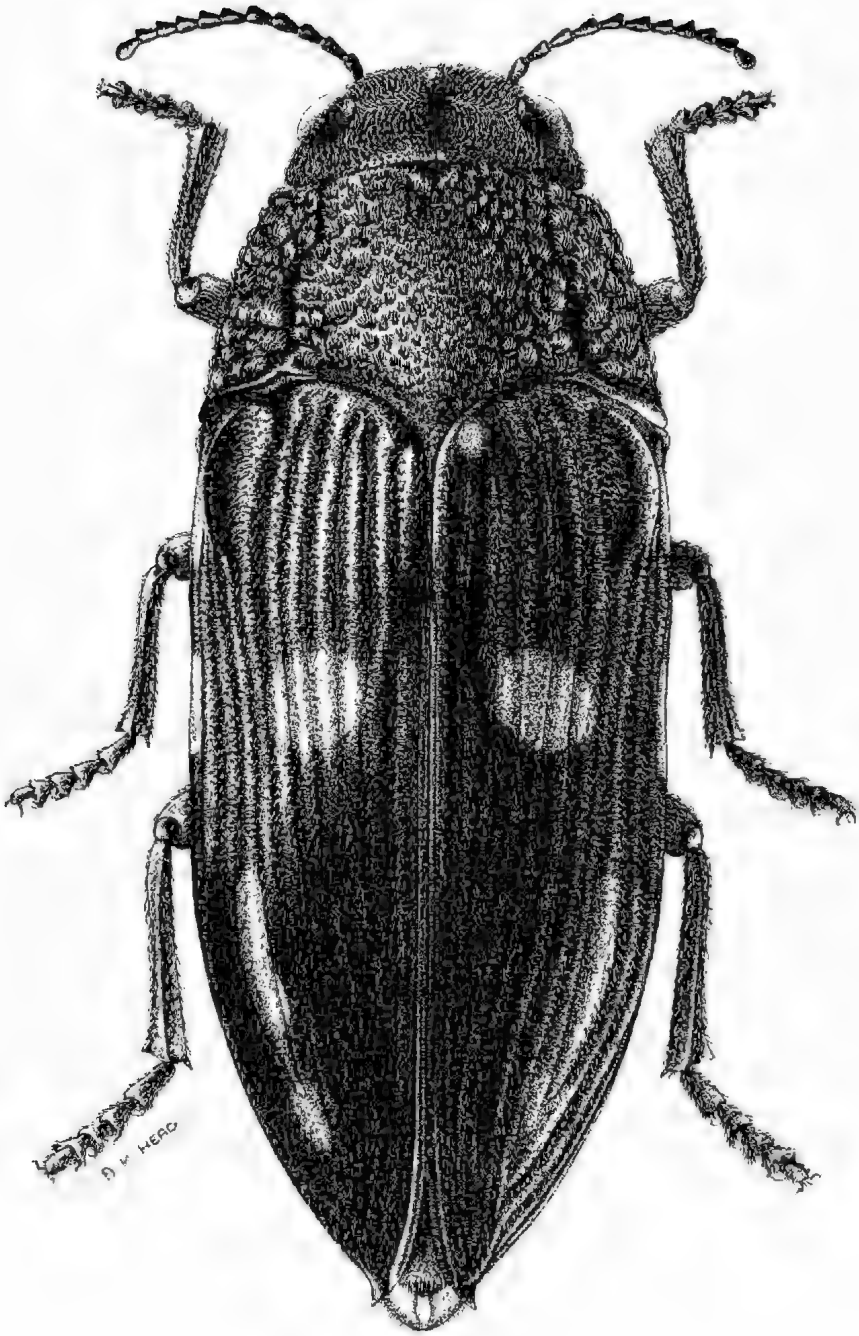
39. *Astraeus (Astraeus) caledonicus* Fauvel, 1904: 116, Obenberger, 1930: 365.

FIG. 20

Type. Holotype: ♀, Baie du Sud, N. Caledonie; Delauney, MNHN (seen by author).

Colour. Upper surface glabrous. Head and pronotum black with green reflections; antennae purple. Elytra black with yellow reflections, each elytron with the following yellow markings: a large basal spot; a small spot after the middle near the suture but not touching it; a spot at the margin covering the humeral fold; a spot after the middle at the margin but not touching it; and slightly behind the last a spot near the suture but not touching it. Undersurface black with green and purple reflections; hairs silver. Legs red-brown with purple reflections; tarsi dark-brown with blue reflections.

Shape and sculpture. Head shallowly but evenly punctured; excavated between the eyes mainly at the apex; no median keel; without hairs. Pronotum shallowly but sparsely punc-



— 5 mm —

Fig. 21. *Astraeus robustus* sp. nov

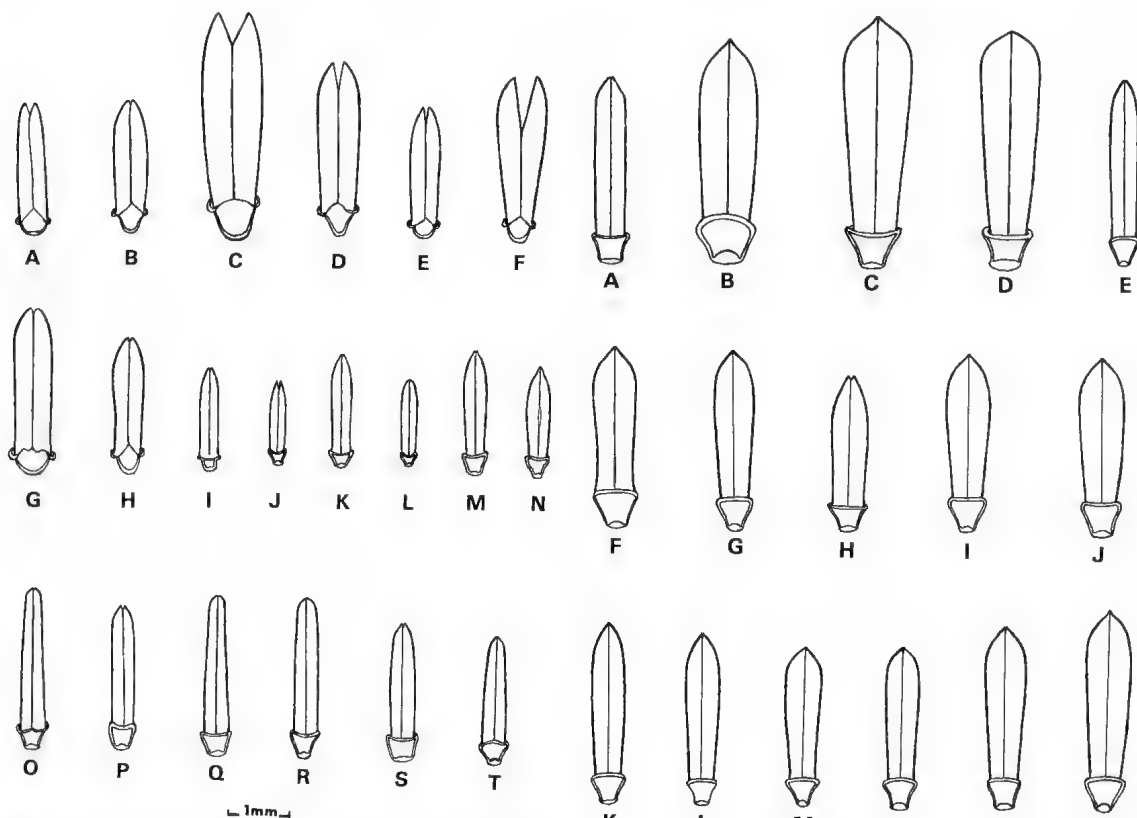


Fig. 22. Outline diagrams of the parameres of male *Astraeus* (*Depollus*) species (A-H) and *Astraeus* (*Astraeus*) species (I-T), dorsal surface uppermost. A-*polli*; B-*tamminensis*; C-*robustus*; D-*aberrans*; E-*lineatus*; F-*multinotatus*; G-*irregularis*; H-*dedariensis*; I-*bakeri*; J-*minutus*; K-*fraseriensis*; L-*pygmaeus*; M-*smythi*; N-*simulator*; O-*obscurus*; P-*globosus*; Q-*mastersi*; R-*samouelli*; S-*dilutipes*; T-*adamsi*.

tured; a short but deeply impressed median longitudinal line projects forwards from the basal crypt; parallel-sided at the base, before the middle rounded and obliquely narrowed to the apex; median lobe short and blunt, apices of lateral lobes sharp and turned downwards. Elytra punctate-striate, the intervals between convex with a few faint transverse wrinkles at the base, without hairs or punctures; parallel-sided until after the middle, then gently rounded to the strong marginal spine; apical

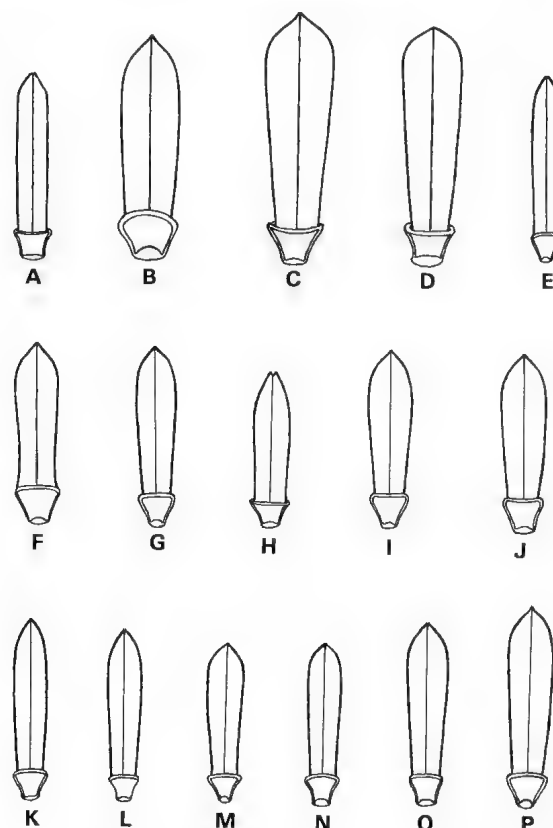


Fig. 23. Outline diagrams of the parameres of male *Astraeus* (*Astraeus*) species, dorsal surface uppermost. A-*intricatus*; B-*crassus*; C-*major*; D-*navarchis*; E-*fraterculus*; F-*prothoracicus*; G-*elongatus*; H-*vittatus*; I-*flavopictus*; J-*macmillani*; K-*carnabyi*; L-*badeni*; M-*jansoni*; N-*oberthuri*; O-*carteri*; P-*goerlingi*.

spine with a straight internal edge; humeral fold rounded and barely obvious. Undersurface shallowly and sparsely punctured; lightly haired.

Size. Females 11.5 x 4.1 mm (1).

Distribution. New Caledonia.

General remarks. *A. caledonicus* shows close affinity with *A. cyaneus*.

Specimens examined. Type only.

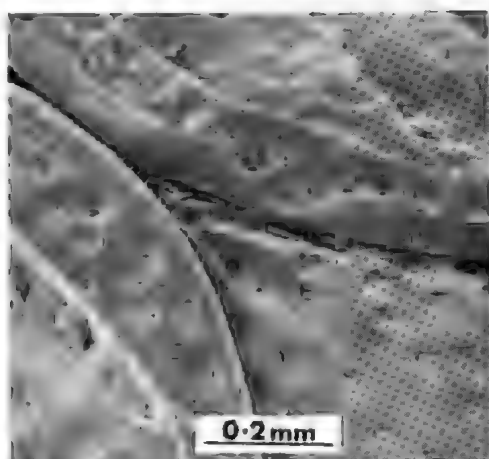


Fig. 24. Scanning electron micrograph of the median lobe of the pronotum of *A. fraseriensis* showing the basal crypt.

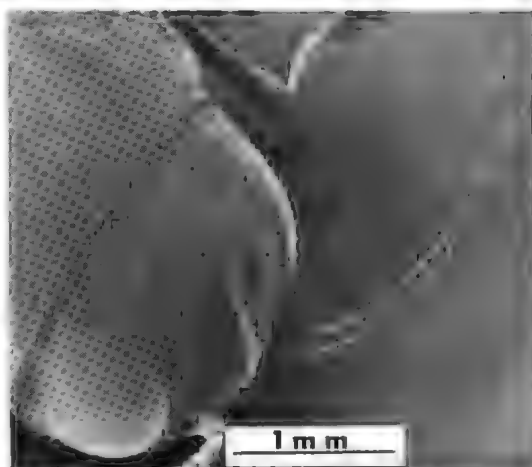


Fig. 25. Scanning electron micrograph of the head of *A. fraseriensis* showing the median longitudinal keel.

Index

TO THE VALID SPECIES AND SYNONYMS OF *ASTRAEUS*, WITH THE NUMBERING SYSTEM ADOPTED IN THE TEXT

| Valid Species | Synonyms |
|--------------------------------------|--|
| <i>aberrans</i> van de Poll 4 | |
| <i>adamsi</i> sp. nov. 20 | |
| <i>budeni</i> van de Poll 32 | = <i>meyricki</i> Blackburn |
| <i>bakeri</i> sp. nov. 9 | |
| <i>caledonicus</i> Fauvel 39 | |
| <i>earnabyi</i> sp. nov. 31 | |
| <i>carteri</i> sp. nov. 36 | |
| <i>crassus</i> van de Poll 22 | |
| <i>cyaneus</i> Kerremans 38 | |
| <i>dedariensis</i> sp. nov. 8 | |
| <i>dilatipes</i> van de Poll 19 | = <i>strandli</i> Obenberger |
| <i>elongatus</i> van de Poll 27 | |
| <i>flavopictus</i> LaPorte & Gory 29 | |
| <i>fraseriensis</i> sp. nov. 11 | |
| <i>fraterculus</i> van de Poll 25 | |
| <i>globosus</i> sp. nov. 16 | |
| <i>goerlingi</i> sp. nov. 37 | |
| <i>intricatus</i> Carter 21 | |
| <i>irregularis</i> van de Poll 7 | |
| <i>jansonii</i> van de Poll 33 | = <i>tepperi</i> Blackburn |
| <i>lineatus</i> van de Poll 5 | |
| <i>macmillani</i> sp. nov. 30 | |
| <i>major</i> Blackburn 23 | |
| <i>mastersi</i> MacLeay 17 | = <i>splendens</i> van de Poll = <i>simplex</i> Blackburn |
| <i>minutus</i> sp. nov. 10 | |
| <i>multinotatus</i> van de Poll 6 | |
| <i>navarehii</i> (Thomson) 24 | |
| <i>oberthuri</i> van de Poll 34 | |
| <i>obscurus</i> sp. nov. 15 | |
| <i>polli</i> sp. nov. 1 | |
| <i>prothoracicus</i> van de Poll 26 | |
| <i>pygmaeus</i> van de Poll 12 | |
| <i>robustus</i> sp. nov. 3 | |
| <i>samouelli</i> Saunders 18 | |
| <i>simulator</i> van de Poll 14 | |
| <i>smythi</i> sp. nov. 13 | |
| <i>tamminensis</i> sp. nov. 2 | |
| <i>virgatus</i> van de Poll 28 | |
| <i>watsoni</i> sp. nov. 35 | |

Acknowledgments

I would like to thank the following people for their assistance: Mr G. Gross, Dr E. Mathews and Mrs B. K. Head, South Australian Museum; Dr E. B. Britton, C.S.I.R.O., Division of Entomology; Mr K. Dahms, Queensland Museum; Mr A. Neboiss, National Museum of Victoria; Dr C. N. Smithers and Dr D. K. McAlpine, Australian Museum; Mr L. Koch, Western Australian Museum; Mr B. Levey and Miss C. M. von Hayek, British Museum; Monsieur A. Descarpentries, Paris Museum; Dr G. A. Samuelson, Bernice P. Bishop Museum; Dr J. Jelinek, National Museum of Prague; Mr K. T. Richards, Western Australian Department of Agriculture; Mr A. George, Western Australian Herbarium; Mr E. Slater, Canberra; Mr E. E. Adams, Edungalba; Mrs J. Harslett, Amiens; Dr F. H. Uther Baker, Applecross; Mr R. P. McMillan, Cottesloe; Mr and Mrs K. Carnaby, Wilga. Dr K. Bartusek, Dr S. J. Edmonds, Dr E. Wollaston, Miss R. Altmann, Miss B. Jones and Mr P. G. Kempster all of the University of Adelaide. The National Parks Board of Western Australia for permission to collect in Flora Reserves; the Director, National Parks and Wildlife Service of South Australia for permission to collect in National Parks. The Royal Society of South Australia provided a grant to cover the cost of one illustration. The Australian Biological Resources Committee provided a grant-in-aid of research.

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FACTORS AFFECTING THE DISTRIBUTION OF THE LEPTODACTYLID FROG *GEOCRINIA LAEVIS* IN THE SOUTH-EAST OF SOUTH AUSTRALIA

*BY R. G. BECK**

Summary

BECK, R. G. (1975).-Factors affecting the distribution of the leptodactylid frog *Geocrinia laevis* in the south-east of South Australia. *Trans. R. Soc. S. Aust.* 99(3), 143-147, 30 August, 1975.

Geocrinia laevis (Günther), a species of leptodactylid frog previously recorded from Victoria and Tasmania, was first reported in South Australia in 1966. A survey has revealed that this new population is an extension of that known to exist in south-west Victoria. The frog is, extremely rare in South Australia, occupying only a fraction of the potential habitat for which it shows preference. Some thoughts on this are tendered as a basis for further studies.

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Introduction

The leptodactylid frog *Geocrinia laevis* (Günther) has been described in detail by Littlejohn & Martin (1964). The specimens found in the south-east of South Australia have been up to 25 mm long, with dorsal skin dark grey and slightly warty, ventral skin smooth and paler grey. All had distinctive pink markings on the groin and thighs and some specimens showed this colour under the forearms as well.

Prior to 1966, *Geocrinia laevis* was known to exist in four disjunct populations in Australia: Tasmania, King Island, the Grampians, and the area in south-west Victoria from Dartmoor to Port Campbell (Fig. 1). With the discovery (Woodruff & Tyler 1968) of a specimen from Marsh's Swamp near Mt Burr, some 80 km west of Dartmoor, it was desirable to establish whether this was a fifth isolate or an extension of the Victorian population.

Methods

The study area comprises the following Hundreds in County Grey: Mt Muirhead, Mayurra, Riddoch, Hindmarsh, Grey, Young, Nangwarry, Mingbool, Blanche and Gambier, and the adjoining area east of the state border to the Glenelg River.

The survey was undertaken from 1968 to 1974, and most areas were visited in both summer and winter. In the early stages of the

survey, field work was concentrated around Marsh's Swamp (Site 3, Fig. 1. Grid reference 353362, Australian Army Survey Map, Penola, 1:250,000 Sheet SJ/54-6). From here the survey extended to the north-west, following the general zone of influence of the Reedy Creek drainage system, and to the south-east along the Dismal Swamp complex to the Glenelg River. Most field work was carried out during the daylight, but night road surveys were conducted in likely areas, yielding one specimen only.

When six specimens had been found, detailed botanical surveys were made of the surrounding areas, particularly of the nearest probable breeding site. Following the establishment of definite ecological patterns, soil surveys of these areas were undertaken.

Typical habitats

Geocrinia laevis normally lays eggs in areas which later become flooded. Breeding sites may be the edges of permanent swamps, or non-permanent swampy areas, often situated to the east of sandy rises, ranging from a few to 200 m away. The soils of the rises are podsolised sands, usually Mt Burr sands as described by Stephens *et al.* (1941). The swamps occur in Wandillo sands, and there may be several intermediate soil types between the rises and the swamps. For this reason, the natural dry sclerophyll forest may vary in type

*Lynwood Park, Mil Lel, S. Aust. 5291.

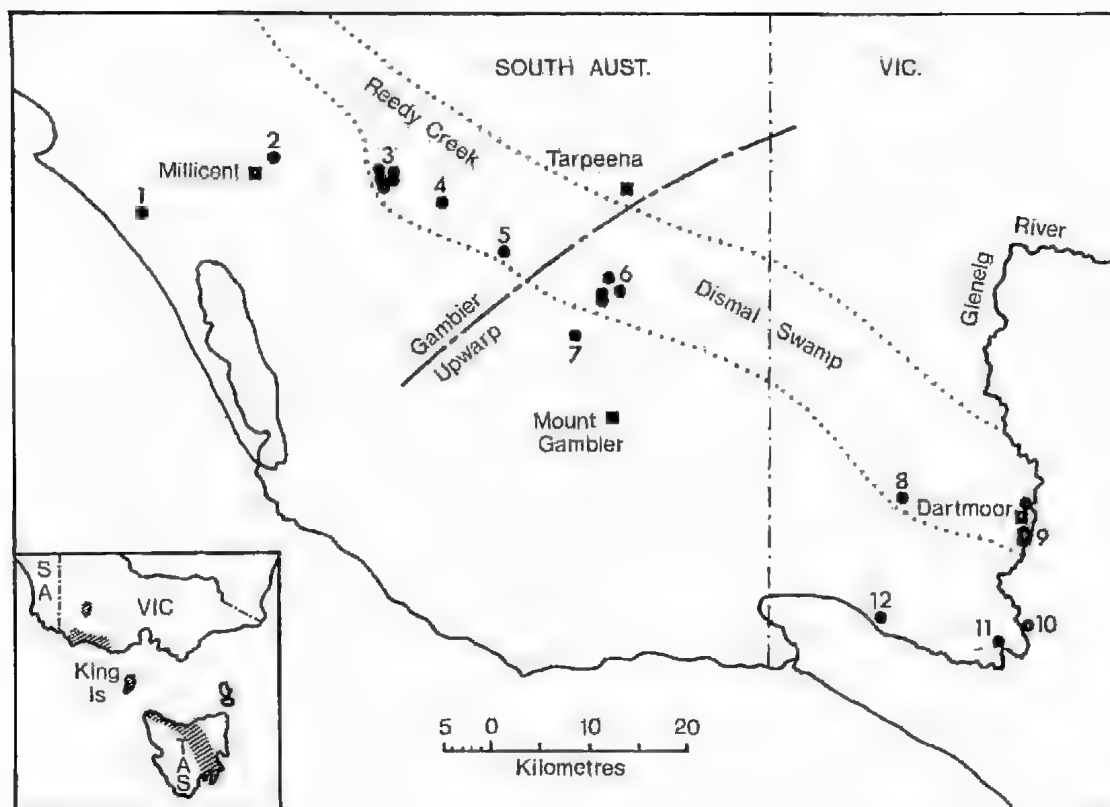


Fig. 1. Map of the lower south-east of South Australia and adjacent south-west Victoria, showing main collecting sites of *Geocrinia laevis* in relation to the Reedy Creek-Dismal Swamp Corridor. The inset shows known Australian distribution prior to 1966. (After Littlejohn & Martin 1964, 1965.)

and consist of any of *Eucalyptus baxteri*, *E. obliqua*, *E. hubertiana* or *E. ovata* according to the soil type. However, the understorey in the vicinity of the swamps is remarkably constant, and four species have been found in all areas, viz. *Acacia melanoxylon*, *Leptospermum juniperinum*, *Melaleuca squarrosa* and *Helichrysum dendroides*.

The soil map of Stephens *et al.* (1941) plus the plant indicator species greatly facilitated later survey work and most potential areas in the south-east have now been examined.

Results

A total of 20 specimens of *G. laevis* have now been found in South Australia, and a further 10 in Victoria between the State border and the Glenelg River, which, prior to 1966, represented the known western limit of distribution. The species is common at Dartmoor, where on one occasion, 12 were found under a log in the bed of the Glenelg River.

Details of the findings are given in Table 1. Representative specimens have been lodged with the S.A. Museum.

Of particular interest is the specimen collected at Grid ref. 376346 (site 7, Fig. 1), in a deep pit dug to observe pine tree root growth at the Forest Research Station north of Mt Gambier. This site is two km from the nearest potential breeding area, giving an indication of the actual mobility of the species, which is regarded as sluggish compared with other local species.

The distribution is shown in Fig. 1, and with one exception corresponds with normal dispersals from the Reedy Creek and Dismal Swamp complexes. It is suggested that the Canunda specimen (site 1, Fig. 1) is from a community established from eggs or larvae washed down one of the many man-made drains which cross the area between the Millicent Hills and the coast.

TABLE 1

Recorded distribution of Geocrinia laevis in south-east South Australia and nearby Victoria
Refer A.A.S. Map, Penola, 1:250,000, Sheet SJ/54-6

| Grid Reference | Site No. (Fig. 1) | No. of Specimens | Collector | Remarks |
|---|-------------------|------------------|------------------------|--|
| 353362 | 3 | 1 | H. Minchan & C. Taylor | First S. Aust. specimen, SAM, R8118 |
| 353362 | 3 | 1 | D. Woodruff | Melbourne University Zoology Dept. 220/67 |
| 353362 | 3 | 6 | R. Beck | All within 2 km of original site at Marsh's Swamp |
| 353362 | 3 | 3 | D. Klem | Marsh's Swamp. One specimen, SAM, R10583 |
| 354364 | 3 | 1 | F. Aslin | 2 km NE of original site at Marsh's Swamp |
| 381351 | 6 | 1 | C. Taylor | Earl's, 16 km N of Mt Gambier |
| 381353 | 6 | 1 | R. Beck | Hein's scrub, 17 km N of Mt Gambier |
| 378351 | 6 | 1 | F. Aslin | Telford's scrub |
| 378349 | 6 | 1 | D. Klem | 2 km S of Telford's scrub |
| 376346 | 7 | 1 | D. Klem | Forest Research Station, Soil Pit, SAM, R13974 |
| 368355 | 5 | 1 | D. Klem | Hogarth's scrub |
| 326360 | 1 | 1 | J. Aslin | Canunda Reserve, SAM R13975 |
| 342366 | 2 | 1 | F. Aslin | Night Road Survey, 5 km NE of Millicent |
| 361361 | 4 | 1 | A. Rowley | Lake Leake, SAM, R14199 |
| Refer A.A.S. Map, Hamilton, 1:250,000, Sheet SJ/54-7 | | | | |
| 414325 | 8 | 6 | P. Roach | 16 km E of State Border on Highway No. 1, SAM, R10780 |
| 414325 | 8 | 1 | R. Beck | Same locality |
| 427324 | 9 | Many | R. Beck | Common in Glenelg River 2 km up and downstream from Dartmoor |
| Refer A.A.S. Map, Portland, 1:250,000, Sheet SJ/54-11 | | | | |
| 428311 | 10 | 1 | F. Aslin | East of Glenelg River near Jones' Lookout |
| 409313 | 12 | 2 | F. Aslin | Lower Glenelg River |
| 424310 | 11 | 2 | J. Aslin | Lower Glenelg River |

The major geological and physiographic features of the region have been described by Sprigg (1952). The Reedy Creek and Dismal Swamp complexes are separated geologically by the Gambier Upwarp, and flow in wet years to the north-west and south-east respectively. However, the watershed gradient is so gradual, being only a few cm per km, that in extremely wet years such as 1896 and 1946 there was an almost continuously wet corridor from the Kingston district to the Glenelg River. Even in years of normal rainfall, swamps are close enough to provide ready access for frogs to the lower south-east from the Glenelg River.

The last occasion on which the Dismal Swamp actually flowed was in 1946, emptying

into the Glenelg River just north and south of Dartmoor by way of the Scott and Ardno Creeks.

In the study area, *G. laevis* is restricted to areas receiving an average annual rainfall of 700 mm or more, whereas in Tasmania and Victoria it is found where rainfall is greater than 500 mm (Martin 1967). If the species in South Australia followed the Victorian rainfall pattern, it would be reasonable to expect the distribution to extend laterally about 100 km. Likewise, if it occupied all sites considered suitable on the basis of soil and vegetation patterns, an extended distribution pattern could be expected to the extent of about 50 km.

Discussion

Three facts emerge from the survey:

1. While it is certain that more specimens will be discovered within and beyond the present known range of distribution, *G. laevis* is extremely rare in south-east South Australia. Even at Marsh's Swamp, where most specimens have been found, I have not positively identified its calls during the April-May-June breeding season, when calls are commonly heard at Dartmoor, Victoria. However, Woodruff & Tyler (1968) have reported the recording of a mating call at Marsh's Swamp.
2. According to present known records, the species occupies only a fraction of the potential habitat for which it shows preference with respect to soils, vegetation and rainfall.
3. *G. laevis* was always found under the shelter of logs, litter, or stones during the day. As a result, the species has not been found in areas cleared for agriculture or pasture production.

Some suggestions for the reason for this restricted distribution are tendered as a basis for further work by someone with more time and resources than the present author. Rainfall and associated weather patterns are probably the major factors influencing the spread of any frog species. In 1967, an extreme drought was experienced in the lower south-east of South Australia. The average annual rainfall at Mt Gambier is 776 mm, but in that year only 402 mm fell, and unofficial figures from the Dismal Swamp area were as low as 280 and 330 mm respectively. In this single dry year, many of the local swamps previously considered permanent, dried up completely, and most of the non-permanent swamps stayed dry throughout the winter. As a result, none of the spring breeders bred, and only a few of the autumn and winter breeders actually spawned.

Since Crocker & Wood (1947) first presented evidence for a recent arid period, many workers have commented, and they are about equally divided in their acceptance or rejection of the concept (Mulvaney & Golson 1971; Littlejohn 1967).

Gentilli (1961) had already offered an explanation for this diversity of opinion: "Australia is a large land, spanning several major climatic belts, and may have experienced different climatic changes in various parts of the

continent at the same time." This is supported, on a one year basis at least, by an examination of the Commonwealth Bureau of Meteorology rainfall figures from major Australian mainland centres for 1967. Perth, Brisbane, Darwin, Cairns, Brisbane and Sydney had greater than average rainfall, Geraldton and Alice Springs were only slightly lower than average, whereas Adelaide and Melbourne received approximately half their average amount. The coastal strip from the head of the Great Australian Bight to east of Melbourne obviously was the worst affected area.

Churchill (1968) has shown that, in Western Australia, during the past 5000 years there have been several fluctuations in climate of sufficient magnitude to cause the replacement of jarrah forests with karri and *vice versa*. Similarly, recent work by Dodson (1974) in the study area indicates variations in climate, with relatively dry periods between 5000 and 2000 B.P., and again since 1300 B.P.

Gentilli (1972) also supports the concept of changing climate. "It must be stressed that climate, being the result of numerous variables variously combined in space and time, can vary, fluctuate, oscillate, or just change." It follows that changes such as these must produce equally dramatic changes in the local fauna.

With pluvial conditions prevailing in southern Australia during the last glacial period, Bassian species extended their range (Littlejohn 1967) and it is reasonable to expect that *G. laevis* occupied much of the lower south-east of South Australia. With the return of present-day weather conditions, its range would have decreased but not to the limits found today. It is therefore suggested that in the recent past, possibly much more recently than that postulated by Crocker & Wood (1947), there has been a period sufficiently arid to cause the withdrawal of *G. laevis* and perhaps some other anuran species to the more favoured parts of south-west Victoria or even the Grampians. It must be emphasised that in this context the term "arid" is relative rather than absolute.

Reoccupation of the south-east of South Australia by *G. laevis* would have occurred by way of the Glenelg River and the Dismal Swamp when wetter conditions returned. This may have taken place even as recently as with in historic times.

Since the settlement of the south-east of South Australia by white man, the area reached its physically wettest state in 1896. This information was obtained from S.E. Drainage Board records and also, some years ago, from old residents who remembered the district during the nineties. They claimed "you could row a boat across country from Kingston to the Glenelg River". While this is no doubt a slight exaggeration, it is surely significant to the distribution of frogs.

Colville & Holmes (1972) attribute the increase of wetness during the second half of the nineteenth century to the clearing of natural scrub. Subsequent widespread planting of pines and establishment of drainage schemes have greatly reduced surface waters.

Very recent reoccupation of the south east by *G. laevis* as outlined above would account for the limited spread of the species. Further

distribution has been prevented by a combination of clearing the natural habitat, and the drying out of the district by drainage, pine plantations and the establishment of better pastures. It is obvious that much more study is required to explain satisfactorily this limited distribution.

Acknowledgments

The author gratefully acknowledges the collection of specimens by the following members of the South East Field Naturalists' Societies: Mr and Mrs F. Aslin, Messrs D. Klem, P. Roach, C. Taylor, and Miss A. Rowley. Also thanks are due to Mr M. J. Tyler and Dr M. Littlejohn for advice and encouragement, and to Mr D. Lewis from the S.A. Dept. of Agriculture for his help with soil identification. The Royal Society of South Australia Inc., kindly granted \$50 towards petrol expenses.

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THE THALLUS AND SPORE DEVELOPMENT OF *LOBOSPIRA BICUSPIDATA* ARESCHOUG (DICTYOTALES: PHAEOPHYTA)

BY TIKVAH EDELSTEIN* AND H. B. S. WOMERSLEY†

Summary

EDELSTEIN, TIKVAH & WOMERSLEY, H. B. S. (1975).-The thallus and spore development of *Lobospira bicuspidata* Areschoug (Dictyotales: Phaeophyta). *Trans. R. Soc. S. Aust.* **99**(3), 149-156, 30 August, 1975.

The apical growth of *Lobospira bicuspidata*, release of tetraspores, and growth of the spores in culture to plants up to 1 cm across, are described. Both development of the axes and growth of the sporelings is from a marginal row of apical cells, and the thallus is monopodially developed. *Lobospira* is therefore placed in the Zonarieae group of the Dictyotales.

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Introduction

Lobospira bicuspidata Areschoug is a distinctive brown alga referred to the Dictyotales. It occurs from Nickol Bay, Western Australia, around southern Australia to Eden, N.S.W., and around Tasmania (Womersley 1967, p. 215) and is frequently abundant in regions of moderate to strong water movement, from just below low tide level to 35 m deep.

The alga (Fig. 2A) is easily recognized by its spirally twisted axes, with a phyllotaxis of about 1/3, bearing laterals with bicuspid, determinate ramuli (Harvey 1858, pl. 34), and with lower branches bearing recurved attachment tendrils. Kjellman (1897, pp. 295, 297) and Oltmanns (1922, p. 185) considered that the thallus develops from an apical cell, with sympodial branching, and *Lobospira* has thus been considered as a member of the Dictyotaceae. The sporangia, about 100 μ m in diameter, occur scattered over the thallus (Fig. 2B); they are developed from cortical cells and sunken in the thallus (Fig. 1B). Neither division of the sporangia nor release of spores has been previously reported, and release was only obtained by the present authors on the one occasion. Sexual reproductive cells also have never been observed. While *Lobospira* has usually been placed in the Dictyotales, and the Dictyotaceae (Womersley 1967, p. 215), its relationships have not been established.

This paper reports observations on apical development, spore release and early growth

of the thallus, made in 1972 while the first author was on leave at the University of Adelaide.

Methods

Plants (ADU, A42264) were collected in drift at Aldinga reef, South Australia, on 27 May, 1972, and transferred to the laboratory in sea water. The specimens (Fig. 2B) bore mature sporangia, many of which released tetrads of spores. Fertile branches were placed in a glass jar with Provasoli ES medium (Starr 1971, p. 359) in a 15°C culture room, and spores allowed to settle on slides during the next two days. On day 3 the slides with attached sporelings were transferred to petri dishes (5 cm in diameter), and germanium dioxide at a concentration of 5 p.p.m. added to the medium. Single sporelings from the slides were detached to be grown in free culture; they were washed several times in a well-slide and inoculated into a new set of dishes each with 15–18 sporelings. After 4 weeks, cultures were maintained in SWM 3 medium (Chen, Edelstein & McLachlan 1969).

As the sporelings developed, considerable difficulty occurred with bacterial (and at one stage fungal) contamination. Addition of penicillin to the Provasoli medium had little effect, but streptomycin (100–150 mg streptomycin sulphate/l of seawater) eliminated most of the bacteria, and a commercial fungicide, Mycostatin-Dusting Powder (1,000,000 units) (E. R. Squibb & Sons Ltd, Melbourne) proved

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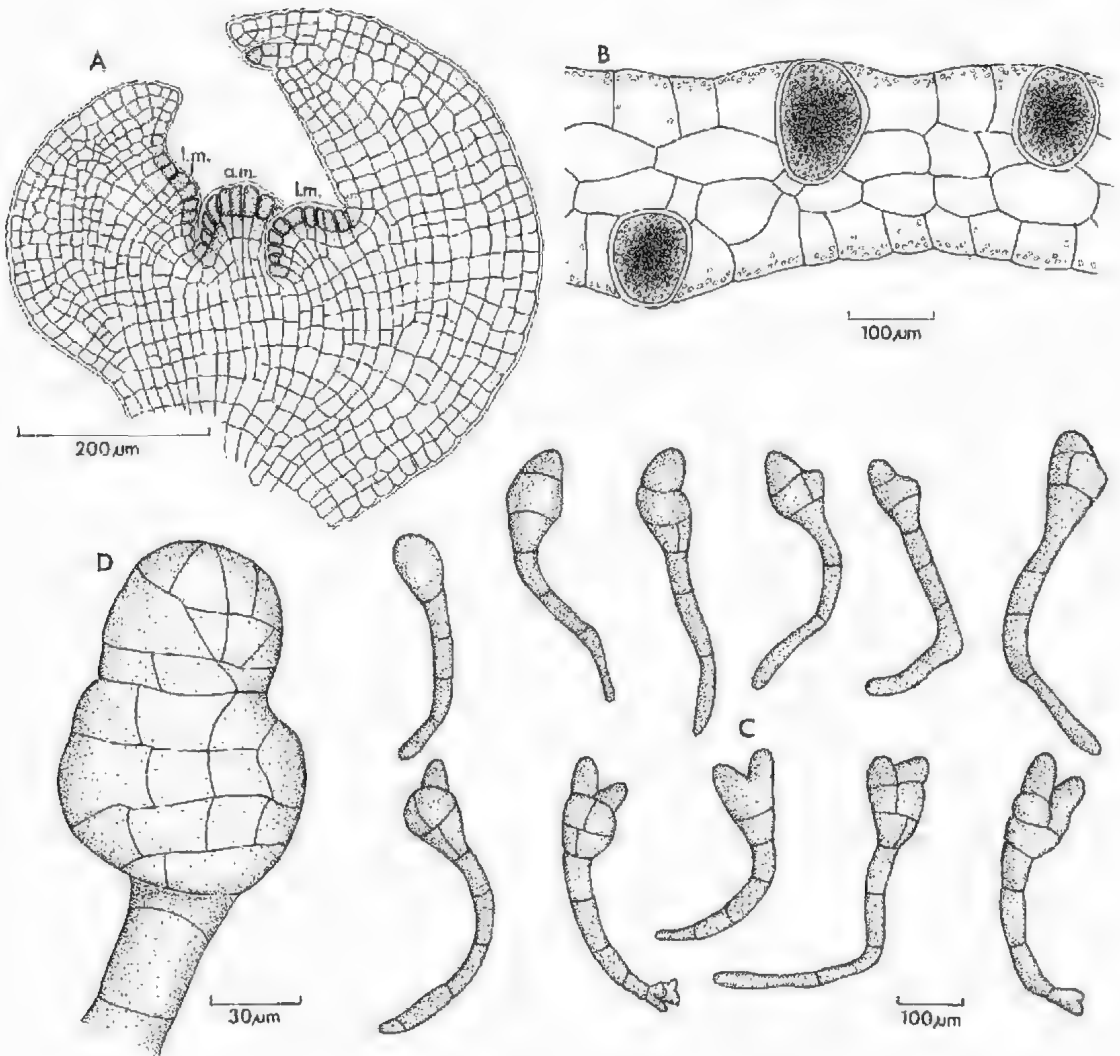


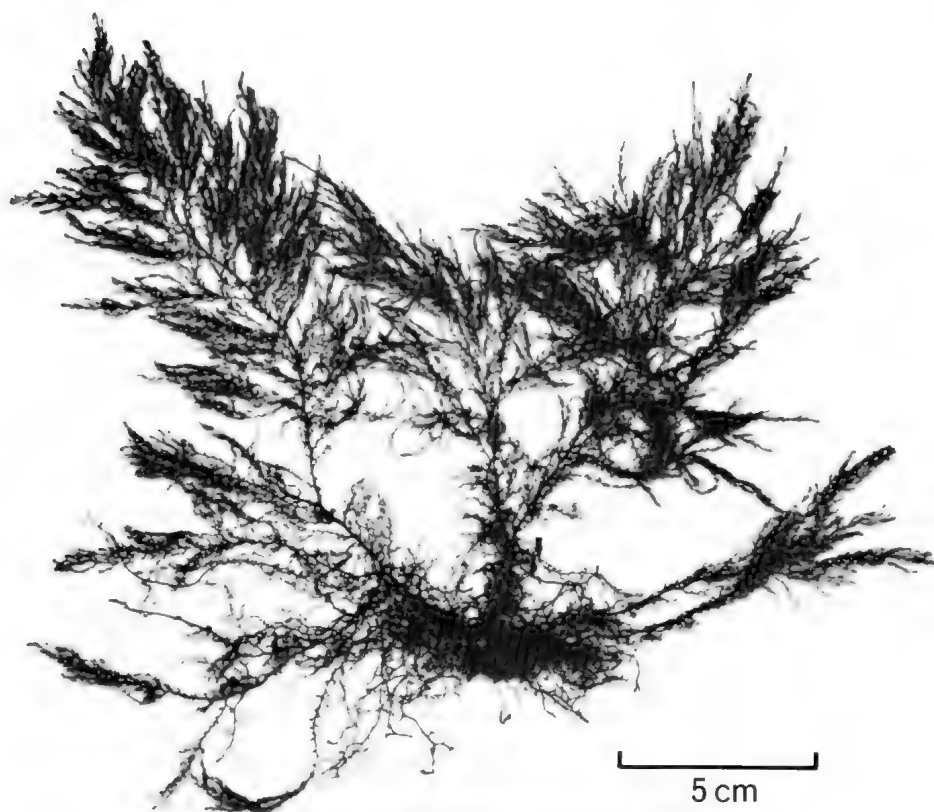
Fig. 1. *A*. Apical development, with two young laterals present, the older one (right) becoming hicuspid. The axis meristem (a.m.) continues growth of the branch, and the lateral meristems (l.m.) may or may not develop further into laterals (ADU, A42264).
B. Cross section of ramulus bearing sporangia (ADU, A42264).
C. Various sporplings 1 week old, with a rhizoid 3-5 cells long and early stages of the "cell-mass".
D. A sporpling 3 weeks old, with a well developed cell-mass.

to be effective when used as a single treatment of 200 mg of "Mycostatin" per 100 ml of sea water for 20 hours. Repeated treatments with streptomycin and Mycostatin were used and frequent cleaning of the sporplings with glass needles was carried out. While this damaged some sporplings, the majority survived and con-

tinued to develop to plants consisting of clusters of branches up to 1 cm across, but from which it was impossible to clean the epiphytes.

In general, cultures were maintained at 15°C under a light intensity of 600-800 lux provided by 40 watt white fluorescent lights, and a regime of 14 hrs light/10 hrs dark. The me-

A



B

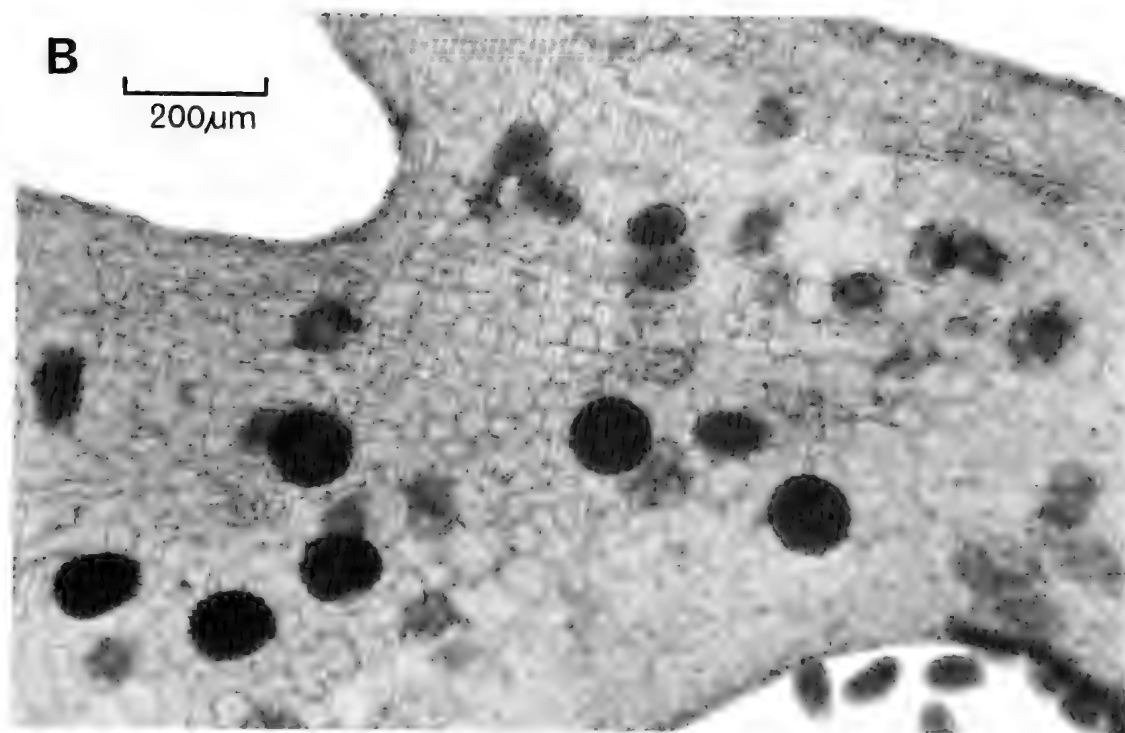
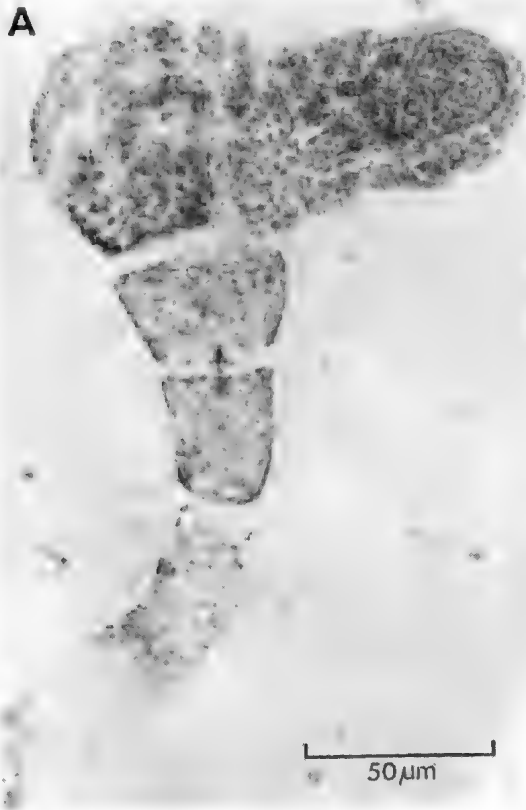


Fig. 2.

A



B



C



D



Fig. 3.

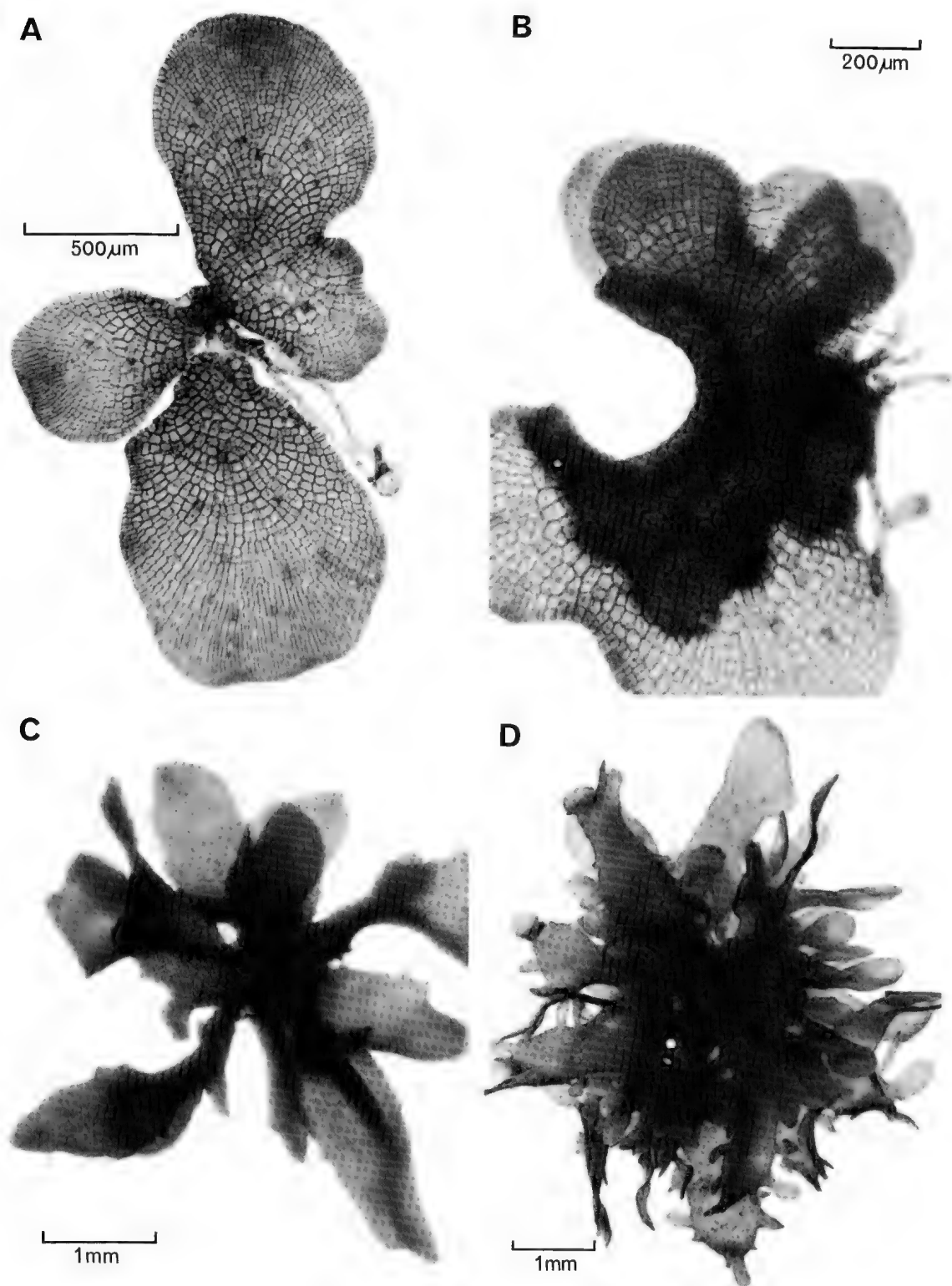


Fig. 4.

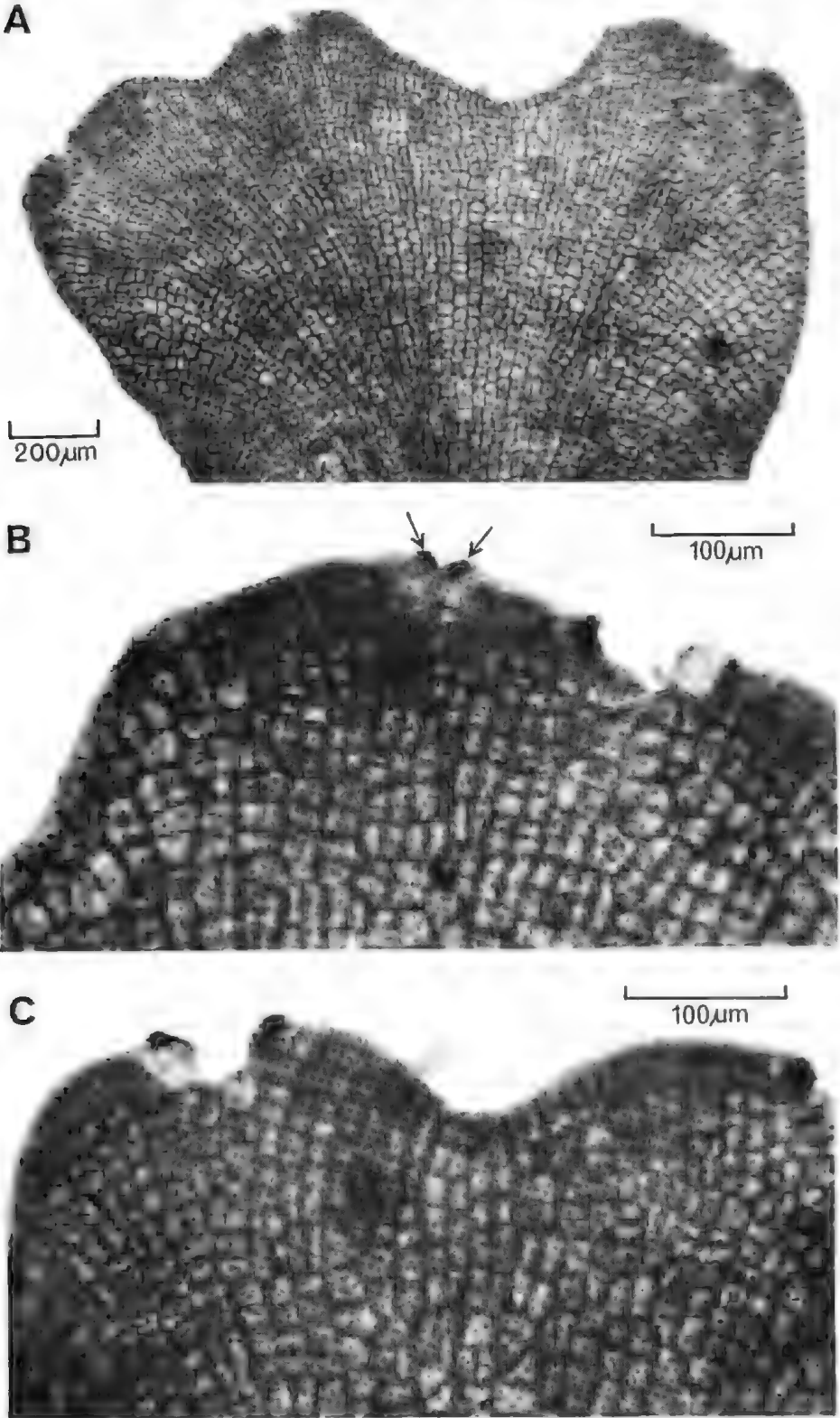


Fig. 5.

- Fig. 2. *A* Thallus of *Lobospira*, showing basal entangled branches with tendril-bearing laterals, and erect branches with ultimate bicuspid ramuli. Stanley Beach, Kangaroo I., S. Aust. (Edelstein & Kraft 126, 25.iv.1972).
B. Surface view of a branch showing tetrasporangia (undivided) and released tetraspores (arrow). (ADU, A42264.)
- Fig. 3. *A*. A multicellular sporcling, with rhizoid, about 2 weeks old.
B. A plant about 3 weeks old, showing development of a flat thallus with a meristematic margin.
C. Plant 6 weeks old, with two lobes.
D. Plant 6 weeks old, showing development of lobes from the margin and especially from the rhizoidal region.
- Fig. 4. *A*. Plant 7½ weeks old, with 3 main lobes.
B. Plant 7½ weeks old, becoming convolute.
C. Plant 12½ weeks old, with several irregular lobes.
D. Plant 17½ weeks old, consisting of many irregular branches, each with marginal lobes of various sizes.
- Fig. 5. *A*. Plant 24½ weeks old: general view of meristematic apex, with degenerating cells in centre of each lobe.
B. As in *A*, with two darkly-staining cells (arrows) separating in centre of margin of lobe.
C. As in *A*, with degeneration of cells between two darkly-staining cells.

dium was changed every 3-5 days for the first 6 weeks and thereafter at weekly intervals.

Results

Development of the thallus

Dissection of apices (Fig. 1*A*) of mature field plants of *Lobospira* shows that development is from a row of apical cells, from which lateral groups of apical cells separate off alternately and differentiate rapidly to form a larger, abaxial, spinous or bicuspid process with a group of meristematic cells on its adaxial side. Growth is thus monopodial and the affinities of *Lobospira* are with the Zonarieae. In actively growing apices, the young laterals develop rapidly and overtop the apex. The meristematic group of cells on the lateral may persist indefinitely, in which case a long lateral develops; or it may persist to give a short lateral with only a few pointed ramuli; or it may not develop further, resulting in only a pointed or bicuspid ramulus, at the apices of which a single cell remains prominent (Fig. 1*A*). Alternate series of these ramuli fringe the longer axes or branches.

The indefinite axes twist spirally so that the branches or ramuli become arranged with a phyllotaxis of about 1/3.

The mature thallus consists of a cortical layer of cells which are arranged more or less in longitudinal lines and tend to radiate upwards. The medulla consists of cells of similar size but rather irregularly arranged (Fig. 1*B*), and is 2-5 cells thick; in older branches a

slight midrib is present where the medulla is thicker. Older axes are ovoid to round in section and a central core of narrower and more elongate cells may be present. Hair groups are of frequent occurrence on the thallus.

Sporangia and spore development

Division of the sporangia into four, tetrahedrally arranged, non-motile spores (Fig. 2*B*) appears to occur only shortly before their release, and no divided sporangia have been observed in any herbarium material. Fertile collections have been made mainly in autumn (April to June).

The spores germinated on slides within two days of their release, forming a short rhizoid which was cut off by a cross wall when slightly longer than the spore. The rhizoid became 3 or 4 cells long before the spore-residual cell enlarged and divided. By day 7, a variety of cell arrangements (Fig. 1*C*) was present amongst the sporelings, which, during the next 2 weeks, developed into elongate-ovoid masses of cells (Figs 1*D*, 3*A*), their arrangement depending on the early cell divisions.

From this cell mass, which was attached by a relatively long rhizoid of several cells, a flat, ovate-spathulate disc of cells developed, mostly two cells thick and with a distinct apical row of meristematic cells (Fig. 3*B*, plant 3 weeks old). During the next 4-5 weeks, further rhizoids developed from the basal cell mass, and the flat, erect, frond developed further from the apical meristem, usually becoming lobed (Fig. 3*C*). Smaller lobes developed both from the

basal cell mass and lower parts of the erect fronds (Fig. 3D).

By 8 weeks, the plants had developed several fronds (Fig. 4A) of varying sizes and often the main frond was becoming convoluted (Fig. 4B). Tufts of long, colourless hairs differentiated at this stage of development. By 12 weeks, numerous fronds were present (Fig. 4C), usually branched or lobed, and thalli 17½–24½ weeks old formed a cluster of fronds (Fig. 4D) up to 1 cm across. One plant reached almost 2 cm across after 34 weeks but showed no further morphological development. At this stage, all thalli were heavily overgrown with epiphytes and died. Apart from the meristematic and lateral margins, the fronds were mostly two cells thick, increasing to 3 or 4 cells thick in the older parts.

The apical marginal row of meristematic cells was prominent in all branches and lobes, giving a typical "zonarioid" appearance (Fig. 5A). Plants 24½ weeks old showed a further apical development of possible significance, in that centrally along the meristematic margin of each lobe, two cells became more prominent (Fig. 5B) with denser protoplasm, and breakdown of tissue occurred between them (Fig. 5A, C). Whether this was only a breakdown feature before death is uncertain, but the two cells concerned, which when first noticeable were densely protoplasmic and appeared healthy, could possibly correspond to the single

cells which are prominent at the apex(ices) of the single or bicuspid ramuli of the mature plant.

Conclusions

The division of sporangia to give four non-motile spores, and the occurrence of a marginal row of apical cells in both the adult axes and in juvenile stages, indicate that *Lobospira* is correctly placed in the Dictyotales, but belongs in the Zonariaceae and not the Dictyotaceae. The distinctive morphology of *Lobospira* separates it generically from all other genera of the Zonariaceae.

While the sporcling and juvenile stages are now known, further studies are necessary to show how such stages develop to the mature laterals which cut off pointed or bicuspid ramuli. Since sexual plants are still unknown, cytological studies on the division of the sporangia are desirable to indicate whether meiosis occurs at this stage.

Acknowledgments

The second author acknowledges a grant from the Australian Research Grants Committee for technical help, and the assistance of Mrs E. L. Robertson and Miss C. G. Anderson with the culture work and illustrations. Dr G. T. Kraft assisted in early stages of the study.

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**TRANSACTIONS OF THE
ROYAL SOCIETY
OF SOUTH AUSTRALIA
INCORPORATED**

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HYDROIDS OF BRUNY ISLAND, SOUTHERN TASMANIA

BY JEANETTE E. WATSON*

Summary

WATSON, Jeanette, E. (1975).-Hydroids of Bruny Island, southern Tasmania. *Trans. R. Soc. S. Aust.* **99**(4), 157-176, 30 November, 1975.

A systematic collection of the sublittoral hydroids of Bruny Island, southern Tasmania, using SCUBA, yielded 34 species, including three newly described, three new records for Australian waters and 11 new records for Tasmania.

Most Haleciidae, including two new species, are epizoic, occupying sheltered microhabitats. Few species of Sertulariidae are recorded, and *Amphisbetia operculata* is now rare in a former habitat. The Plumulariidae is represented mainly by small epiphytic forms, and *Plumularia angusta*, *P. crateriformis* and *P. wilsoni* are recorded for the first time from one locality. Two species newly described, *Halecium bruniensis* and *H. luteum*, are each closely related to endemic New Zealand species. The occurrence of these, and the first record of *Salacia farquhari* outside New Zealand waters (where it also occurs south of 43's) suggests active progress of speciation and dispersal across the Tasman Sea.

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Introduction

Bruny Island (43°25'S, 140°20'E) is situated off the east coast of Tasmania, 25 km south of Hobart. The island is approximately 50 km long and is separated from the Tasmanian mainland by the narrow waters of the D'Entrecasteaux Channel. The indented coastline of Bruny Island provides a range of environmental conditions varying from the sheltered but swift flowing tidal waters of the D'Entrecasteaux Channel to the rough-water eastern coastline of Adventure Bay and Penguin Island, open to the Tasman Sea.

Systematic collecting of the sublittoral hydroid fauna was undertaken during two weeks in February, 1972. Sampling, using SCUBA equipment, was carried out over the entire depth range (0-20 m) presented by the rocky sublittoral along the coastline at Satellite Island, Great Taylor Bay, Simpsons Bay, the adjacent D'Entrecasteaux Channel, and at Fluted Cape, Penguin Island and Adventure Bay on the eastern coastline of Bruny Island.

No collection was made of hydroids from the littoral zone, as these localities comprise either steep rocky cliffs facing the Tasman Sea or the sandy beaches of the D'Entrecasteaux Channel. It is unlikely that either of these biotopes would make any significant contribution to the hydroid fauna of Bruny Island.

topes would make any significant contribution to the hydroid fauna of Bruny Island.

In his revision of the hydroid fauna of Tasmania, Hodgson (1950) listed 64 species known from the deep and shallow waters of the Tasmanian coast and Bass Strait. His list includes 22 species from the D'Entrecasteaux Channel and the adjacent Derwent Estuary, and one species from Adventure Bay.

The present survey yielded 34 species (including two identifiable only to genus) and 2 varieties of one species. There are 11 new records for Tasmania, including 3 new records for Australia, and 3 species are newly described. Only 19 species of Hodgson's list appear in the present collection.

Holotype and paratype microslides of new species, and other microslides and material, are lodged in the National Museum of Victoria, Melbourne (referred to as NMV).

No athecate hydroids were recorded from Bruny Island. The Campanulariidae is represented by 5 species, Lafoeidae by 1, Haleciidae 6, Syntheciidae 1, Sertulariidae 9, and the Plumulariidae by 12 species, including 2 varieties of one species.

LIST OF SPECIES

* Denotes a new record for Tasmania

† Denotes a new record for Australia

* National Museum of Victoria, Russell Street, Melbourne, Vic. 3000.

THECATA

Family CAMPANULARIIDAE

- * *Campanularia ambiplica* Mulder & Trebilcock.
- * *Campanularia pulcrathea* Mulder & Trebilcock.
- Clytia* sp.
- Orithopyxis caliculata* Hincks.
- Silicularia rosea* Meyen.

Family LAFOEIDAE

- * *Hebella ?furax* Millard.

Family HALECIIDAE

- Halecium delicatulum* Coughtrey.
- Halecium* sp.
- * *Halecium beanii* (Johnston)
- Halecium brauiensis* n.sp.
- Halecium luteum* n.sp.
- Phylactotheca armata* Stechow.

Family SYNTECHIIDAE

- Synthechium patulum* Busk.

Family SERTULARIIDAE

- + *Saldacia farquharii* (Bale).
- Stereotheca elongata* (Lamouroux).
- Sertularella robusta* Coughtrey
- Symplectoseyphus pygmaeus* Bale.
- Sertularia acuta* (Stechow).
- * *Sertularia macracarpa* Bale.
- Amphisbetta minima* var. *intermedia* Bale.
- Amphisbetta operculata* (Linnaeus).
- Amphisbetta ayia* n.sp.

Family PLUMULARIIDAE

- Halicornopsis elegans* (Lamarck).
- * *Aipenella campanuliformis* (Mulder & Trebilcock).
- Pycnotheca mirabilis* var. *mirabilis* (Allman).
- Halopteris campanula* var. *campanula* (Busk).
- Plumularia filiculilis* Kirchenpauer.
- * *Plumularia hyalina* Bale.
- * *Plumularia angusta* Stechow.
- * *Plumularia crateriformis* Stechow.
- * *Plumularia wilsoni* Bale.
- Aglaophenia plumosa* Bale.
- Thecocarpus divaricatus* var. *typica* (Busk).
- * *Thecocarpus divaricatus* var. *briggsi* Bale.
- Halicornaria longirostris* (Kirchenpauer).

Systematic Section

Family CAMPANULARIIDAE

- Campanularia ambiplica* Mulder & Trebilcock, 1914a: pl. 2, figs 3, 4. Shepherd & Watson, 1970: 140.**

Paracalyx ambiplica Stechow, 1925: 209, fig. E.

Record: Penguin I., on a red alga and sponge in crevices on rough-water side of island, 16–20 m deep.

Material: Colonies infertile. Hydrothecae with 7 fairly sharp teeth, the embayments between wider than the teeth.

Remarks: Although occurring on the rough-water side of the island, this small delicate

species occupied a microhabitat in sheltered crevices at a depth below turbulence due to surge.

This is the first record of *C. ambiplica* from Tasmania. Other localities: Victoria; Champion Bay, W. Aust.

***Campanularia pulcrathea* Mulder & Trebilcock, 1914a: 11, pl. 2, figs 1, 2. Blackburn, 1942: 105.**

Paracalyx pulcrathea (Mulder & Trebilcock, 1914a). Stechow, 1923a: 3.

Record: Satellite I. (no depth recorded), on red alga *Delisea*.

Material: Colonies infertile. *Hydrothiza* tubular, stems 0.83–1.33 mm long, 0.06–0.09 mm diam., perisarc thick, a spherule between stem and hydrotheca. *Hydrothecae* long and tubular, perisarc thickening distally, a distinct diaphragm near base and a flexure almost two-thirds the distance up the hydrothecal wall from the base. Margin with 8–10 teeth. Diam. of hydrotheca at margin 0.32–0.41 mm, depth to diaphragm (including teeth) 0.77–0.92 mm.

Remarks: The Tasmanian material compares well with the holotype of *C. pulcrathea* (in NMV), although the present specimens have fewer marginal teeth.

This is the first record of *C. pulcrathea* from Tasmania. Other localities: Victoria; S. Aust.

Clytia sp.

FIG. 1

Record: Adventure Bay, 10 m deep on stem of *Thecocarpus divaricatus* var. *typica*.

Material: A few infertile stems. Stems of variable length, 0.70–1.90 mm, irregularly undulated, in some places smooth. *Hydrothecae* campanulate, expanding from base to margin, perisarc fairly thick, and a well defined diaphragm with a thickening of the thecal wall below. Depth to diaphragm 0.30–0.40 mm. A small spherule between hydrothecae and pedicel. Margin 0.20–0.32 mm diam., with 12 bluntly pointed teeth, the embayments between slightly wider than the teeth.

Remarks: The hydrotheca of this relatively small species corresponds in some respects with *C. hemisphaerica* (Linnaeus, 1767), but the stem lacks the typical proximal and distal annulations of this species. In the absence of gonosome it is not possible to further identify the material.

***Orithopyxis caliculata* (Hincks, 1853). Bale, 1914b: 74, Pl. 11, fig. 1, pl. 12, fig. 1;**

1924: 232. Hodgson, 1950: 7, figs 14-16. Shepherd & Watson, 1970: 140.

Campanularia caliculata Hincks, 1853: 178, pl. 5, fig. 5.

Eucopella caliculata (Hincks). Hirohito, 1969: fig. 6.

Record: Penguin I., 15-20 m deep, on a red alga and on sponge in a crevice.

Material: A few fertile colonies. *Hydrothecae* very shallow and expanding; hydrothecal pedicels spirally annulated, a few with smooth regions. *Hydranth* with 24 tentacles. *Gonotheca* smooth with thick perisarc, containing mature gonophores.

Remarks: The specimens from sponge possess longer pedicels and have a thinner perisarc than those epiphytic on algae.

O. caliculata was not abundant at Bruny Island, occurring only in a sheltered crevice on the rough-water side of the island at a depth below major turbulence. This accords with previous findings on habitat preferences of this species (Shepherd & Watson 1970; Watson 1973).

Silicularia rosea Meyen, 1834: 204, pl. 35, figs 1-11. Millard, 1968: 259.

Silicularia bilabiata (Coughtrey, 1875). Ralph, 1957: 842.

Eucopella campanulifera von Lendenfeld, 1883, Dale, 1888: 751, pl. 13, figs 9-15.

Silicularia campanulifera (von Lendenfeld, 1883); Hodgson, 1950: 6, figs 12, 13.

Record: Fluted Cape (no depth recorded) on the brown algae *Sargassum axillaris* and *Seyothalia dorycarpa*.

Material: Luxuriant fertile male and female colonies on the algae. Developing gonophores present.

Remarks: The present material conforms to descriptions given by Ralph (1956, 1957) for *Silicularia bilabiata* forma *subtropica* (demonstrated by Millard (1968) to be a synonym of *S. rosea* Meyen), a form occurring only north of the Subtropical Convergence, and typical of the southern Australian coastline, including Tasmania.

Family LAFOEIDAE

Hebella ? *furax* Millard, 1957: 200, fig. 8; 1964: 10, figs 2B-D. Millard & Bouillon, 1973: 59.

FIG. 2

Record: Penguin I., on stem of *Thecocarpus divaricatus* var. *typica*, depth 20 m.

Material: One small colony. *Hydrorhiza* a loosely winding tube. *Hydrothecae* large, cam-

panulate, perisarc delicate, smooth. *Hydrotheca* asymmetrical, one side convex, the other straight or slightly concave; this side always inclined to the hydroid host. *Margin* entire, with a thin slightly everted rim. *Pedicel* of variable length, perisarc thick, strongly undulated to smooth, widening distally to pass into base of hydrotheca below diaphragm. Immature hydrothecae truncated with a thin cap-like operculum.

Dimensions (mm):

| | Bruny I. | South Africa |
|-----------------------|-----------|--------------|
| <i>Hydrotheca</i> — | | |
| depth to diaphragm | 0.80-0.92 | 0.74-0.84 |
| diam. at margin | 0.50-0.68 | 0.55-0.65 |
| diam. at diaphragm | 0.14-0.18 | 0.22-0.28 |
| <i>Pedicel</i> | | |
| length from diaphragm | 0.20-0.29 | 0.52-0.72 |
| minimum diam. | 0.05-0.08 | 0.08-0.10 |

Remarks: Comparison of the Bruny I. material with paratype microslides of *Hebella furax* Millard from False Bay, South Africa (provided by Dr N. A. H. Millard) shows that although similar in shape to the South African specimens, the hydrothecae of the Tasmanian material are generally deeper and narrower at the diaphragm, lack the distinct thickening of the lower (hecal) wall, and have a more pronounced eversion of the margin than the South African specimens. However, in the absence of gonophores it is difficult to determine the specific status of hydroids of simple morphology, hence the present specimens are provisionally assigned to *H. furax*.

This is a new record for Australia.

Family HALECHIDAE

Halecium delicatulum Coughtrey, 1876a: 299; 1876b: 26, pl. 3, figs 4, 5. Ralph, 1958: 334, figs 11, 12 (synonymy).

Halecium flexile Allman, 1883: 11, pl. 5, fig. 2. Hodgson, 1950: 16, figs 25-27.

Records: Adventure Bay, Penguin I., Satellite I., on the kelp *Macrocystis pyrifera*, 2-7 m deep; Fluted Cape, 10 m deep, on *Thecocarpus divaricatus* var. *typica* (Busk).

Material: Luxuriant fertile colonies. *Stems* to 1 cm long, simple and branched. Many hydrophores with marginal replications; secondary hydrophores arising from the pedicel of primary hydrophores. Colonies dioecious with mature gonophores arising from proximal parts of stem and on hydrorhiza. Distal parts of blastostyle cap-shaped in both sexes. Colour, trophosome yellow, gonophore bright orange.

Remarks: Hodgson (1950) described and figured *H. flexile* Allman (= *H. delicatulum*)

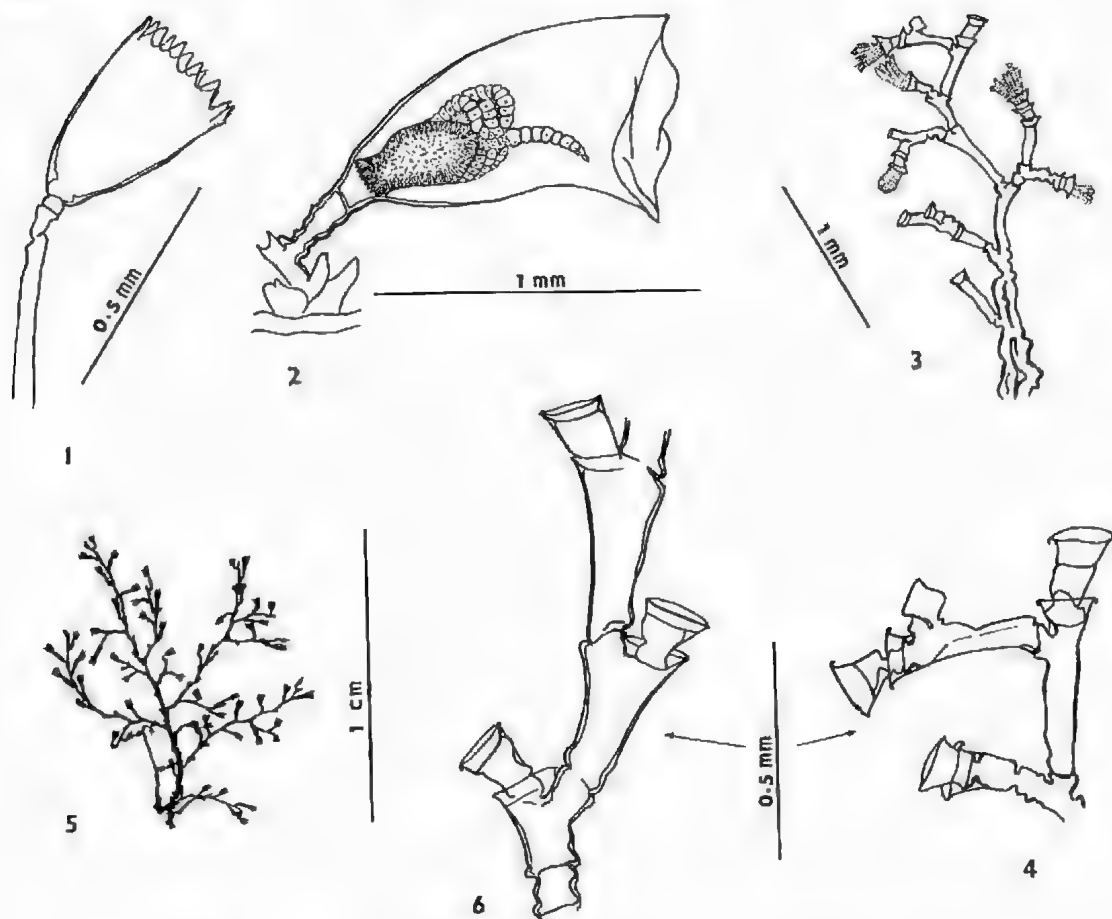


Fig. 1. *Clytia* sp., Hydrotheca.

Fig. 2. *Hebella furax* Millard. Hydrotheca epizoic on *Thecocarpus divaricatus*.

Figs 3, 4. *Halecium* sp. Fig. 3.—Whole colony, Fig. 4.—Distal part of colony enlarged.

Figs 5, 6. *Halecium beanii* (Johnston). Fig. 5.—Whole colony. Fig. 6.—Part of stem showing hydrophores.

from Eaglehawk Neck, but did not record the substrate.

The colonies of *H. delicatulum* in the present collection, while very abundant on *Macrocystis* and other brown algae, were, however, strictly epizoic, always growing on the surface of the crustose bryozoan *Membrinopora membranacea*, a common epiphyte on the aging fronds of *Macrocystis*.

Halecium sp.

FIGS 3, 4

Record: Penguin I., on a red alga in sheltered water, no depth recorded.

Material: One infertile stem. Stem 3 mm high, lightly fascicled at the base, branching irregularly sympodial. Stem internodes of variable length, 0.30–0.40 mm, narrow, perisarc fairly

thick, with one proximal annulation and a distal apophysis giving rise to the succeeding internode. *Hydrophore* fairly deep, expanding to margin, slightly asymmetrical, adcauline wall more expanding than abcauline wall. Depth to diaphragm, 0.06–0.07 mm, depth to base of hydranth, 0.05–0.06 mm, *Margin* 0.12–0.14 mm diam., with a distinct outwardly rolled rim. *Diaphragm* concave, approximately 0.01 mm below line of attachment of hydranth, usually a strong thickening of the inner wall immediately below diaphragm, best seen in older hydrophores, often absent in younger terminal hydrophores. Punctae not visible; if present, obscured by hydranths. Pedicels of hydrophores of variable length; shorter pedicels usually annulated, longer pedicels smooth. Hydrophores regenerated 1–3 times, regenerated pedi-

cels often with a deep proximal constriction, *Hydranth* short and stubby, with approximately 14 tentacles.

Remarks: The single specimen from Bruny I. resembles *H. tenellum* Hinks, 1861, and *Halecium* sp. recorded from Pearson I. (Watson 1973, p. 167). However, *H. tenellum* is monosiphonic and the dimensions given by Millard (1957, p. 193) and Ralph (1958, p. 340) for *H. tenellum* are greater than those of the present material. The specimen from Pearson I., while similar in habit, is monosiphonic, the margin of the hydrophore is more everted, and the overall dimensions are smaller. Without adequate fertile material it is not possible to make a decision on the specific status or relationships of the specimen from Bruny I.

Halecium beaulti (Johnston, 1838). Millard, 1957: 188; 1966: 464; 1968: 256, fig. 9A-F. Ralph, 1958: 332, fig. 10a, b, c-k.

FIGS 5, 6

Records: Adventure Bay (no depth recorded) on encrusting sponge on underside of the red alga *Sonderophycus australis*; Penguin I., 15 m deep, on sponge in crevice.

Material: Busby infertile colonies to 15 mm long. Proximal parts of the colonies fascicled, becoming monosiphonic distally, usually where regrowth has occurred from broken polysiphonic tubes. **Branching** irregular, occasionally tendrils given off distal ends of branches through the orifice of the terminal hydrophore. **Stem** internodes of variable length, 0.28–0.52 mm, narrowest at node, 0.08–0.12 mm, widening distally to 0.18–0.23 mm to accommodate hydrophore. Nodes distinct, with a slightly oblique slope alternately right and left, occasionally straight. **Hydrophores** alternate, shallow, saucer-shaped, adnate to internode, diam. at margin 0.12–0.14 mm. Diaphragm distinct, 0.02–0.04 below margin, tilted towards node, marked by a thickening of perisarc, a ring of punctae (frequently not well seen) above. **Secondary hydrophores** given off on a short pedicel from diaphragm of primary hydrophore, adcauline wall convex, abcauline wall straight or very slightly hulled. Body of hydranth delicate, with approximately 14–16 long filiform tentacles borne on a long peduncle, a deep constriction between peduncle and hypostome.

Remarks: Since the Bruny I. specimens conform to descriptions, and fall well within the range of dimensions given for *H. beaulti* by

Millard (1957) and Ralph (1958), the specimens, although infertile, are assigned to this species.

An unusual microhabitat is the epizoid growth on crustose sponge on the underside of the thick, plate-like thallus of *Sonderophycus*.

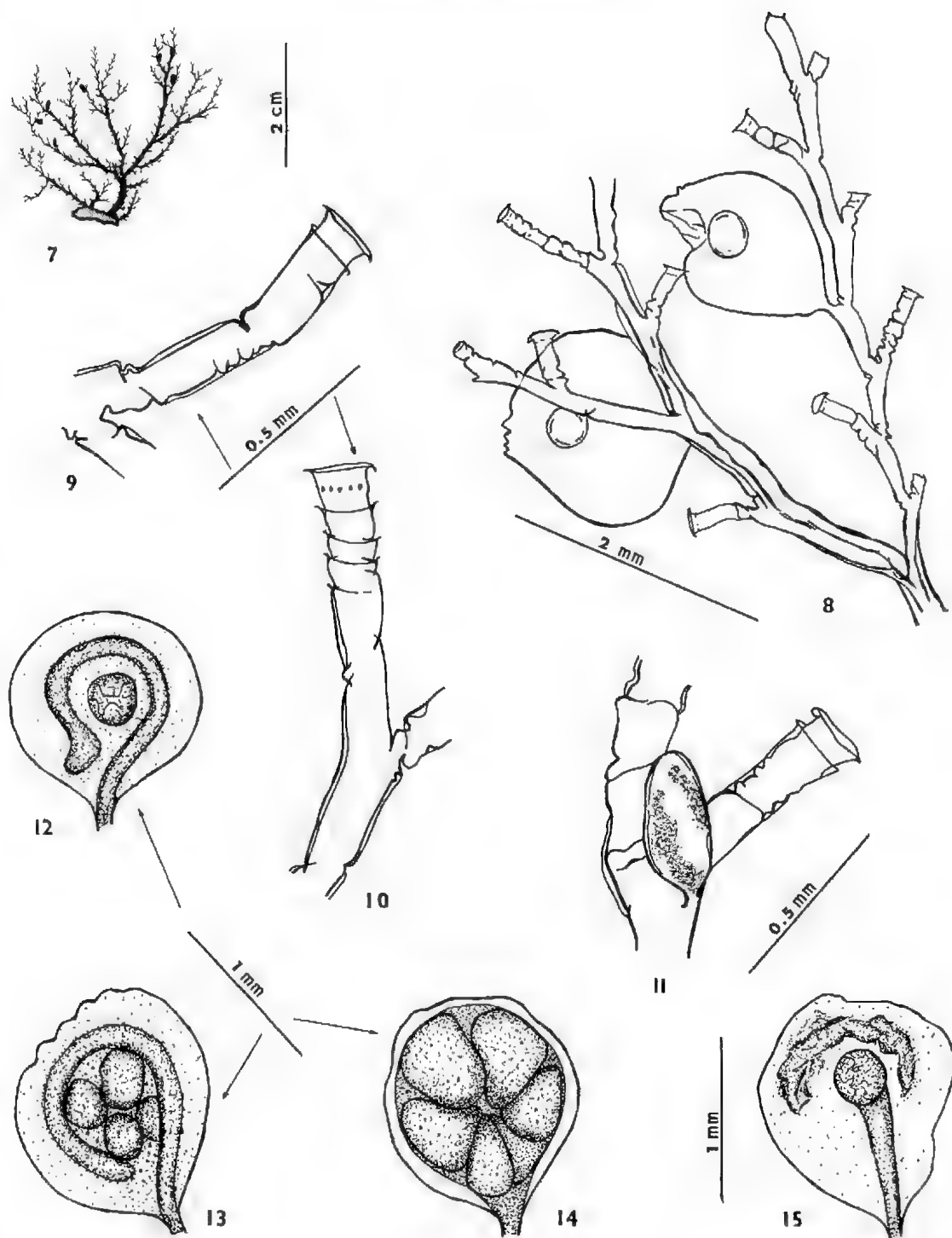
H. beaulti is a cosmopolitan species, not previously recorded from Australian waters. It is rare at Bruny I.

***Halecium brunensis* n. sp.**

FIGS 7–15

Type material and records: Holotype, NMV, G2494-microslide; G2495-preserved material, remainder of holotype colony; Penguin I., 20 m deep, on sponge and bryozoa in crevice.

Description from holotype: **Erect stem** 3 cm high, growth habit arborescent, in one plane, stems sparingly fascicled at base, woody, the polysiphonic tubes running up stem, forming the branches. **Branches** monosiphonic distally, with markedly sympodial growth. **Stem** internodes of ultimate branches of fairly constant length, 0.48–0.64 mm, narrower proximally, widening distally to 0.10–0.12 mm at node. **Nodes** oblique, well defined, sloping alternately left and right, often 1 or 2 annulations above node. **Pedicel** of hydrophore given off distally from a well defined apophysis 0.04–0.14 mm long, at the same level as the node. **Pedicel** tubular, 0.13–0.20 mm long (node to diaphragm), perisarc of younger parts smooth, in older regenerated parts heavily internally ridged, a deep fold just above apophysis giving pedicel an offset appearance. **Hydrophore** fairly deep, 0.06–0.08 mm margin to diaphragm, slightly expanding with an everted margin, 0.15–0.18 mm in diam., and distinct rim. **Diaphragm** well defined, thin, with a ring of punctae just above and a pseudodiaphragm below, frequently only marked by a thickening of the adcauline wall. **Secondary and tertiary regenerations** of the pedicel from the orifice of the preceding hydrophore common, each succeeding pedicel usually shorter than the last; in some instances regeneration is reduced to a mere replication of the hydrophore. **Secondary branching** of pedicels rare. **Hydranth** elongated, slender, with 10–16 long filiform tentacles. **Female gonotheca** very large, flattened, lenticular, but somewhat variable in shape, usually slightly longer than wide; greatest width 0.98–1.33 mm; length (excluding pedicel) 1.20–1.43 mm, tapering proximally into a short pedicel arising at base of hydrophore, usually at junction with main stem. **Perisarc** very delicate,



Figs 7-15.

distal extremity puckered, a small circular orifice sealed by an operculum situated in the distal third of the abcauline wall. *Male gonotheca* small, sausage-shaped, 0.25 mm long, 0.10 mm wide, arising from a short pedicel at base of hydrophore. Both sexes arising only on younger, monosiphonic parts of colony, the males more distal than females. Colour, stems straw coloured, female gonophores pink.

Remarks: *Halecium brunensis* is closely allied to *H. lenticulare* Trebilcock, 1928, in sympodial habit, shape of female gonotheca and hydrotheca. However, *H. lenticulare* as known at present (Ralph 1958, p. 331) is a monosiphonic species with smaller stems (less than 1 cm high), a considerably smaller female gonotheca, and a male gonotheca of somewhat different shape.

The type material of *H. brunensis* shows growth stages of the female gonophore from earliest development to maturity (Figs 12-15). Development of the gonophore begins with formation of a hook-shaped blastostyle surrounding a central body (Fig. 12). Further growth and differentiation into 6-8 large bodies, possibly larvae (but material insufficiently well preserved for positive identification), then occurs, filling gonotheca (Figs 13, 14). A small circular aperture with slightly thickened rim then develops in the distal third of the abcauline wall through which the reproductive products escape (Fig. 15). The orifice of the now empty gonotheca then becomes resealed by a very thin operculum.

Only one group of colonies of *H. brunensis* was found. These were epizoic on sponge and encrusting bryozoa in a sheltered crevice.

Halecium luteum n. sp.

FIGS 16-18

Type material and Records: Holotype, NMV, G2496—microslide (KOH cleared preparation); G2497—preserved material, remainder of holotype colony; paratype G2498—microslide; Penguin I., 15 m deep on sponge and rock.

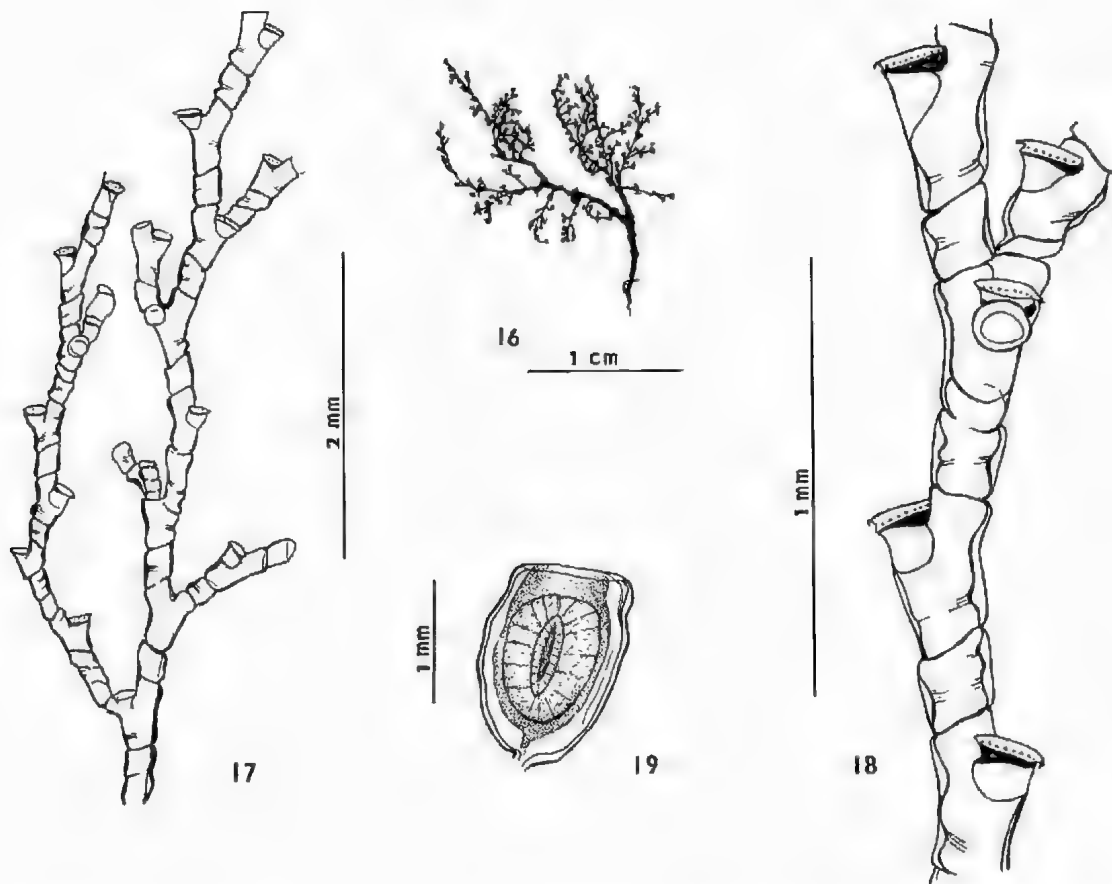
Description from holotype and paratype: Colonies to 2.5 cm high, growth arborescent, main stem strongly fascicled, woody and stiff.

Branching more or less in one plane, the ultimate branches in any one part of the colony all directed anteriorly; in other parts they may face in other directions. *Stem internodes* of variable length, 0.40-0.65 mm, expanding distally, with 1, occasionally 2, extra nodes. *Nodes* distinct, oblique, parallel in each internode, sloping alternately left and right in adjacent internodes; perisarc indistinctly internally ridged. Width at proximal node, measured parallel to node, 0.12-0.14 mm. *Hydrophore* seated on distal third of distal segment of internode, well below node. Hydrophore sessile, very flat and shallow, walls thin and strongly constricted just above diaphragm, abcauline wall more concave than adcauline. *Margin* circular, 0.14-0.16 mm in diam., with outrolled rim. Depth from margin to punctae, 0.015-0.02 mm; depth from margin to diaphragm, 0.025-0.035 mm. Diaphragm very strong, with a distinct ring of punctae above, and a wedge-shaped thickening of the perisarc of the internode below. Below the wedge the wall of the internode thins into a large circular fenestration from which the apophysis of a branch may arise. *Hydranth* large with an annular hypostome and 25-28 tentacles. Colour, bright yellow. Gonotheca, absent.

Remarks: *Halecium luteum* is superficially similar to *H. corrugatissimum* Trebilcock, 1928, from New Zealand, as it has strongly ridged internodes and shallow hydrophores characteristic of this species. In the latter species, however, the ridges of the stem are merely strong annular constrictions, not definite oblique nodes as in *H. luteum*. Furthermore, the hydrophores, while shallow, are somewhat deeper than those of the new species. Also, *H. corrugatissimum* is a monosiphonic species, while *H. luteum* has a strongly fascicled habit.

H. luteum displays several unusual morphological features. One is the presence of supplementary nodes, so well defined that the stems could almost be described as being alternately athecate and thecate; another feature is the extraordinarily shallow hydrophore, which seems to offer negligible support to the very

Figs 7-15. *Halecium brunensis* n.sp. Fig. 7.—Holotype colony, natural size. Fig. 8.—Distal part of colony, showing fasciculation of stem and empty female gonothecae. Figs 9, 10.—Hydrophores enlarged, showing offset pedicel and replications of the hydrophore. Fig. 11.—Male gonotheca. Figs 12-15.—Development of the female gonophore. Fig. 12.—Early stage of development showing hook-shaped blastostyle with developing central mass. Fig. 13.—Later stage of development. Fig. 14.—Mature gonophore. Fig. 15.—Gonotheca after discharge of reproductive products. Note residual mass remaining at site of the circular orifice through which contents have been discharged.



Figs 16-18. *Halcium luteum* n.sp. Fig. 16.—Paratype colony, twice natural size. Fig. 17.—Distal part of branch. Fig. 18.—Stem internodes with hydrophores enlarged. Fig. 19. *Phylactotheca armata* Stechow. Gonothecca with developing male gonophore.

bulky hydranth. The extreme thinning of the wall of the internode in the fenestration below the hydrophore must produce a serious structural weakness of the hydrocaulus. This is, however, offset by the support given to the hydrophore by the very strong wedge of perisarc extending across the base of the hydrophore from the stem.

The group of colonies were both epizoic and epilithic, growing down from the roof of a cavern in sheltered conditions.

Phylactotheca armata Stechow, 1924: 59; 1925: 204, fig. C. Blackburn, 1942: 106. Hodgson, 1950: 17, fig. 31. Watson, 1973: 166. *Ophiodissa fragilis* Blackburn, 1937: 365, fig. 1.

FIG. 19

Records: Penguin I. and Adventure Bay; epizoic on solitary ascidians, bryozoa and sponge; epiphytic on crustose coralline algae and on

holdfasts of *Phyllospora comosa*, 10-22. m deep.

Material: Luxuriant colonies, some fertile. **Stems** of variable length, 4-15 mm, usually simple, occasionally branched. Colonies dioecious, gonophores borne thickly on hydrorhiza at base of stems, gonothecae large, flatly ovate, both sexes of same size and shape, widest at middle or top, perisarc thick, slightly undulating, borne on a very short pedicel, length 1.14-1.56 mm (excluding pedicel), maximum width 0.90-1.17 mm. Gonophores mature, of creamy white colour, almost filling gonotheccal cavity, male surrounded by a thin blastostyle, female packed with mature ova. **Hydranths** with a single row of large lenticular nematocysts (probably stenoteles) alternate with the tentacles surrounding the hypostome. These also occur in the nematocyst batteries in the capi-

tulum of the retracted dactylozooids, and are scattered throughout the hydrocaulus in some stems. No discharged nematocysts were seen.

Remarks: Blackburn (1937) described the gonophore of "*Ophioidissa fragilis*" (= *P. armata*) as being "subspherical, arising at the junction of stem and peduncles, as well as stem and hydrorhiza". Blackburn's type microslide of "*O. fragilis*" (NMV collection) shows three extremely delicate structures which appear to be either directly attached to, or enveloping the hydrocaulus. Although two of these contain a central mass which could possibly be a developing gonophore, they resemble neither in shape or structure the immature and mature gonophores of *P. armata* as seen in the present material. They do, in fact, closely resemble egg capsules of certain minute gastropods.

P. armata shows a wide range of substrate. The epiphytic colonies, particularly those from the rough-water sites among *Phyllospora* hold-fasts, were usually short and robust, with heavily ridged cauline perisarc. Epizoic colonies, particularly those from more sheltered situations under ledges in deeper water, were lax, branched, with a more delicate perisarc and fewer intranodal ridges. All stems, however, show a tendency towards thickening of the perisarc and increase in cauline ridges with age.

This is the most abundant occurrence of *P. armata* so far recorded in Australian waters, and demonstrates a greater variability in stem characteristics than formerly known.

Family SYNTHECHIDAE

Synthecium patulum (Busk, 1852). Hodgson, 1950: 18, figs 32, 33.

Sertularia patula Busk, 1852: 390.

Records: Satellite I., 14 m deep, under ledge; Simpsons Bay, 11 m deep, on scallop *Equichlamys bifrons*; Penguin I., 20 m deep, on sponge.

Material: A few infertile colonies. Stems to 25 mm long, some stems immature. Proximal internodes of stems short, with 1 pair of opposite hydrothecae, followed by an internode with 2 pairs of opposite hydrothecae and distal hydrocladia; distal internodes with either 1 pair or 2 pairs of hydrothecae. Hydrothecae on older stems with thick perisarc and replications of the margin. Colour, purple and white.

Remarks: The present material conforms to descriptions of *Synthecium patulum* given by Bale (1914a, p. 5) and Hodgson (1950). However, it is very difficult (Watson 1973, p. 167)

to distinguish between *Synthecium elegans* f. *subventricosum* and *S. patulum* on characters of the hydrothecae alone. The present material is thus provisionally assigned to *S. patulum*. Further work may eventually prove that the two are conspecific.

No morphological differences could be detected between stems growing in the environmental extremes of exposure to current (Simpsons Bay), sheltered situations under ledges (Satellite I.) or exposure to surge (Penguin I.).

Family SERTULARIIDAE

Salacia farquhari (Bale, 1924). Ralph, 1961a: 769, fig. 7.

FIGS 20-22

Thuiaria farquhari Bale, 1924: 244, fig. 10. Trebilcock, 1928: 19, pl. 8, fig. 4.

Records: Penguin I., 15 m deep; Satellite I., 3 m deep, on sponge under ledge.

Material: Two infertile colonies. Stems monosiphonic, to 18 mm long, simple and branched, the simple stems shortest. Stem internodes tapering proximally and distally, with one pair of opposite hydrothecae adnate in front, widely separated behind. Branching regularly alternate from an apophysis of the internode 0.25-0.4 mm long, usually 2 pairs of hydrothecae between branches. Branches given off at an upward angle with a distinct proximal geniculation at the apophysis and a V-shaped distal joint. Some secondary branching, but where developed, these branches carry few hydrothecae.

Remarks: The specimens compare well with microslides of *Thuiaria farquhari* Bale (NMV collection) and with the redescription of *S. farquhari* given by Ralph (1961a). The present material does, however, exhibit certain differences from the species as described from New Zealand. These are the greater length and the proximal geniculation of the first branch internode, as well as the tendency towards thickening and loss of the stem internodes in older parts of the colonies, features recognized by Ralph as being more characteristic of *Salacia bicalycula* (Coughtrey, 1876a) than *S. farquhari*. Since the present material agrees in most respects with the latter species, particularly in the size of the colonies, it is assigned to *S. farquhari*.

This is the first record of *S. farquhari* for Australia, and the first record of the species outside New Zealand waters, where it occurs only south of 43°S, the same latitude as Bruny I.

Stereotheca elongata (Lamouroux, 1816).
Ralph, 1961a: 762, fig. 4. Watson, 1973:
170.

Sertularia elongata Lamouroux, 1816: 189, pl.
5. Bale 1884: 75, pl. 6, figs 7, 8, pl. 19, fig. 7;
1915: 277. Hodgson, 1950: 23, figs 38, 39.

Record: Penguin I., 15 m deep, on rough-water
side of island, on a red alga.

Material: Several fertile colonies. *Stems* short,
2.5 cm. *Gonothecae* long and narrow, horned
processes very much elongated.

Remarks: Hodgson's Oyster Bay material from
storm-drifted weed is the "long-stemmed" form
of *S. elongata*. The Bruny I. material is the
"short-stemmed" ocean form frequently asso-
ciated with red algae.

Sertularella robusta Coughtrey, 1876a: 300, fig.
2. Hodgson, 1950: 33, fig. 58. Ralph,
1961a: 824, fig. 22a-d. Watson, 1973:
171, fig. 21.

FIGS 23, 24

Records: Satellite I., 3 m deep, on sponge
under ledges, and 6 m deep on the red alga
Sonderophycus australis; D'Entrecasteaux
Channel, 11 m deep on dead seawhip *Primo-
ella australasiae*, and on old scallop shells.
Equichlamys bifrons; Adventure Bay, 5 m deep
on sponge under ledges; Fluted Cape (no depth
recorded) on stem of a brown alga.

Material: *Stems* 3–4 mm long, the longer stems
flexuous, with long internodes, occasionally
branched. Shorter stems robust, with short
internodes, each stem type occurring in
separate colonies. *Hydrothecae* of the "long
internode" form large with smooth, very faintly
undulated walls, hydrothecae of the "short
internode" form distinctly smaller (see dimen-
sions), with thinner perisarc, heavily ridged
with 3–4 annulations and a strong submarginal
constriction of the thecal neck on the abcauline
side. All material infertile except for one stem
of the "short internode" form.

| Dimensions (mm): | long | short |
|-----------------------------|-------------------|-------------------|
| | internode form | internode form |
| Length, abcauline wall | 0.55–0.60 | 0.33–0.45 |
| Length, free adcauline wall | 0.35–0.43 | 0.28–0.38 |

Remarks: Specimens of *S. robusta* from Bruny
I. show a complete range of variability between
the extremes of the long and short internode
forms, and large and small hydrothecae. Some
correlation appears to exist between stem type,
environmental conditions and habitat pre-
ferences, the long flexuous stems growing epi-

zoically on dead shell and other material in
the D'Entrecasteaux Channel in situations of
good current flow, those of intermediate stem
length being from cryptic habitats beneath
ledges and on the underside of *Sonderophycus*,
while the more robust stems occurred on the
lower parts of brown algae in moderately tur-
bulent open water. Dimensions given by Hodg-
son (1950) for his material correspond to the
"short internode" form, although the stems of
his material were 15 mm long, and were epi-
phytic.

Except for the greater thickness of stem
and very faint thecal undulations, the "long
internode" form of the Bruny I. material cor-
responds very closely with *Sertularella simplex*
(Hutton, 1873) described from Pearson I.
(Watson 1973). A specific distinction based on
thickness of perisarc and faintness of undula-
tions of the thecal wall as defined by Ralph
(1961a, p. 820) seems to be somewhat arti-
ficial. Thus, if further material with smooth
hydrothecae and thin perisarc is found, *S.
robusta* must be referred to the synonymy of
S. simplex.

Syniplectoscyphus pygmaeus (Bale, 1881).
Watson 1973: 176.

Sertularia pygmaea Bale, 1881: 25, pl. 12, fig.
9; 1884: 108, pl. 3, fig. 8, pl. 19, fig. 19.
Hodgson, 1950: 36, figs 63, 64.

Record: Penguin I., 16 m deep on bryozoa in
sheltered situations.

Material: Sparse infertile colonies. *Stems* to
7 mm long, simple, or with one branch. A
delicate 3-flapped operculum visible in most
hydrothecae.

Remarks: The line of small dots in the thecal
wall diagnostic of *S. pygmaeus* is obscured by
the hydranths. However, the material corres-
ponds closely with specimens of *S. pygmaeus*
in the Bale collection (NMV) and for this
reason is assigned to this species.

Sertularia acuta (Stechow, 1921). Millard, 1958:
192, fig. 8. Shepherd & Watson, 1970: 140.

Tridentota acuta Stechow, 1921: 231.
Sertularia loculosa Bale, 1884: 91, pl. 4, figs
5, 6; 1913: 121, pl. 12, figs 7, 8; 1915: 272.
Hodgson, 1950: 25, figs 43, 44.

Record: Adventure Bay, 10–22 m deep, on red
algae.

Material: Luxuriant fertile colonies. *Stems* to
7 mm long. *Gonothecae* with 4–6 strong annu-
lations, arising from stem internode below
proximal hydrotheca. Gonophores mature.

Remarks: Hodgson's infertile specimens came from storm-drifted *Macrocystis*. *S. acuta* was not associated with this kelp at Bruny I.

Sertularia macrocarpa Bale, 1884: 80, pl. 5, fig. 2, pl. 19, fig. 11; 1914a: 14; 1915: 277. Mulder & Trebilcock, 1914b: 42. Hodgson, 1950: 27, fig. 47. Shepherd & Watson, 1970: 140. Watson, 1973: 177.

Record: Penguin I., sheltered side, 10–22 m deep, among algal holdfasts.

Material: Rare colonies, comprising a few stems each. Stems to 8 cm long, infertile.

Remarks: The internal submarginal tooth is not as well developed in these specimens as in those from the Australian mainland.

This dark brown species with distinctive white-tipped hydrocladia has previously been recorded among the holdfast fauna of red algae at Pearson I. (Watson 1973).

This is the first record of *S. macrocarpa* from Tasmanian waters.

Amphisbetia minima* var. *intermedia Bale, 1915. Watson, 1973: 179, fig. 29

FIG. 25

Sertularia minima Thompson, 1879: 104, pl. 17, fig. 3. Bale, 1881: 21, 45, pl. 12, fig. 2; 1884: 89, pl. 4, figs 9, 10, pl. 19, figs 12, 13; Mulder & Trebilcock, 1914b: 39; Hodgson, 1950: 23, figs 41, 42.

Records: Adventure Bay, 4–6 m deep, on red alga *Rhodymenia* and on sponge under ledges; Penguin I., 16 m deep, on red algae and in crevices in rough water; Satellite I., 1 m deep, on *Laurencia*.

Material: Luxuriant fertile colonies, mainly on red algae, some on sponge. Stems to 5 mm long, internode length 0.30–0.38 mm; diam. at node 0.03–0.06 mm. *Hydrotheca* 0.19–0.28 mm long. *Tubular nematothecae* present in the base of proximal infrathecal chamber.

Remarks: Although the hydrothecae are larger than those recognized as var. *intermedia* (Watson 1973, p. 181), the present material is referable to this variety on the basis of the shape of the hydrothecae and the presence of the characteristic tubular nematothecae. However, several of the stems have rather robust hydrothecae and the wedge of perisarc between hydrocaulus and hydrotheca considered typical of the var. *pumiloides*. Furthermore, one stem (Fig. 26) from sponge, shows distinct transitional features between the *pumiloides* and *intermedia* types. The stem of this specimen has four broad, robust, proximal hydrothecae

of "*pumiloides*" type, and a distal regrowth of three hydrothecae of unmistakably "*intermedia*" type following stem breakage. The basal pair of "*intermedia*" hydrothecae have well developed tubular nematothecae. Dimensions of the proximal and distal groups of hydrothecae on this stem are given for comparison:

| Dimensions (mm): | <i>pumiloides</i> type | <i>inter- media</i> type |
|---------------------|---------------------------|---------------------------------|
| Internode— | | |
| length | 0.33–0.35 | 0.30–0.34 |
| width at node | 0.06 | 0.04 |
| Hydrotheca— | | |
| length | 0.20 | 0.21 |
| width across base | 0.24–0.25 | 0.18–0.20 |
| width across margin | 0.43–0.52 | 0.32–0.37 |

The finding of two varieties of *A. minima* on one stem lends support to evidence (Watson 1973) that these varieties are in reality ecomorphs, the development of which may be dependent upon the type of substrate available, or environmental conditions prevailing during growth.

Hodgson (1950) did not differentiate between the varieties of *A. minima* in his collections; however, according to his measurements, and the absence of nematothecae, as well as the material having come from *Macrocystis* and "drift" (brown?) algae, the material may be ascribed to the "*var. pumiloides*".

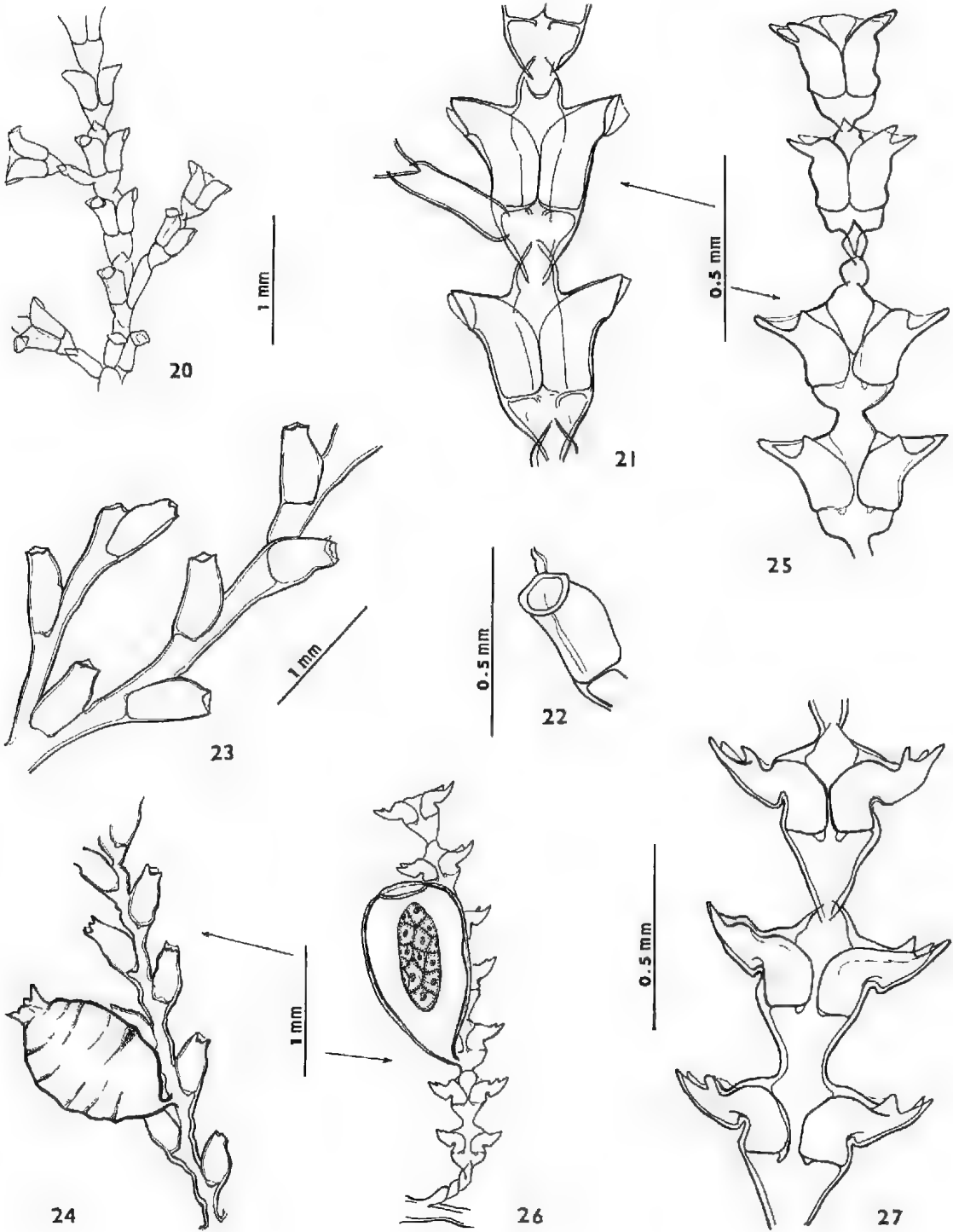
Amphisbetia operculata (Linnaeus, 1758).
Ralph, 1961a: 775, fig. 8.

Sertularia operculata Linnaeus, 1758: 808. Bale, 1884: 67, pl. 6, fig. 1, pl. 19, fig. 3. Hodgson, 1950: 22, figs 36, 37.

Record: Simpsons Bay, 11 m deep on stem of dead seawhip *Primmocella australasica*.

Material: One small infertile colony of a few short stems.

Remarks: Although Hodgson remarks that "this species is very abundant in the D'Entrecasteaux Channel, being constantly taken in the form of large tangled masses in scallop dredges", only one colony was found in the present survey. This apparent rarity may be due to seasonal growth (Hodgson's material was collected in August) or to permanent changes in the environmental equilibrium caused by scallop dredging. The substrate of old shells preferred by *A. operculata* (pers. observ.) is no longer available as the seafloor of the estuary has now been invaded by enormous numbers of the New Zealand gastropod *Maoricolpus roseus*. Since no colonies of *A. operculata* were found associated with *M. roseus*, it may be concluded that the smooth



Figs 20-27.

shell of this gastropod is unsuitable for settlement of larvae of *A. operculata*.

***Amphisbetia avia* n. sp.**

FIGS 26, 27

Type Material and Records: Holotype, NMV, G2499—microslide; G2500—preserved material, remainder of holotype colony; Adventure Bay: paratypes, G2501, G2502—microslides; Satellite I., all colonies on the brown alga *Carpoglossum confluens*, 3 m deep.

Description from holotype and paratypes: *Hydrothiza* tubular, 0.09 mm diam., reticulate, very loosely wound on algal surface. Stems arising at stolonial junctions, simple, unbranched, to 5 mm long, beginning with 1 or 2 twists, then a V-shaped proximal joint, followed by first thecate internode. Perisarc of stem and hydrothecae thick and very brittle. *Stem internodes* 0.38–0.46 mm long, with one pair of hydrothecae, nodes slender, 0.06–0.08 mm wide; distal node collar-shaped, proximal node V-shaped and socketted into the collar of preceding internode; if node absent, it is replaced by a narrowing of the internode. *Hydrothecae* opposite, on distal half of internode, tubular, narrowing to margin, adnate for one third of length, proximal adcauline wall more or less parallel to axis of internode, in contact or slightly separated, base of hydrotheca horizontal; a very deep notch, and occasionally a short oblique intrathecal fold about one third distance up abcauline wall from base of hydrotheca, and a corresponding, but not so deep inflexion (sometimes missing altogether) of the adcauline wall, opposite; but more distally situated, just behind margin. Width of internode just below hydrotheca, 0.24–0.29 mm; length of fixed adcauline thecal wall (measured diagonally) 0.15–0.19 mm, length of free adcauline wall (to end of tooth) 0.12–0.18 mm; length of abcauline wall (measured diagonally from base to end of tooth) 0.26–0.31 mm. *Margin* horizontal, facing upwards, with two long, sharp, laterally placed teeth with a deep horizontal embayment between, connected to the internode by a thick wedge of perisarc.

Width across margin between teeth 0.07–0.09 mm; width across paired hydrothecae (outermost teeth) 0.52–0.69 mm. A delicate internal sheath often present within margin. *Gonothecae* large, obovate, 1.15–1.33 mm long (including pedicel) expanding from base to summit; max. width 0.75–0.83 mm, tapering evenly into a narrow pedicel arising from the infrathecal chamber of hydrotheca on lower stem. *Aperture* circular, 0.35 mm in diam., centrally situated at distal end, with a slightly raised collar, a ring of minute denticles within, and a flat operculum. *Gonothecae* identical in both sexes, only one borne on each stem; male and female gonophore on same colony. Female gonophore narrowly elliptical, not filling gonothecal cavity, with 16–20 eggs; male gonophore of same shape and size as female, spermatogenic mass surrounded by a thin blastostyle.

Remarks: *Amphisbetia avia* is closely related to the *Amphisbetia minima* group in size, colour, habit, and preference for algal substrate, and is not easily distinguished from the varieties of *A. minima* in the field. However, the deep retroflexion of the abcauline wall, the horizontally directed distal part of the hydrotheca, and the long marginal teeth immediately distinguish *A. avia* from *A. minima*.

A. avia was associated only with one species of alga, *Carpoglossum confluens*, growing in shallow water.

Family PLUMULARIIDAE

***Halicornopsis elegans* (Lamarck, 1816).** Bale, 1914a: 56; 1915: 303; Briggs, 1914: 296; 1915: 309; Blackburn, 1942: 107; Hodgson, 1950: 48, fig. 79; Watson, 1973: 195. *Plumularia elegans* Lamarck, 1816: 129.

Record: Adventure Bay, 15 m deep, epilithic on vertical face.

Material: One fertile colony. *Stems* short, to 7 cm, *Gonothecae* borne prolifically on main stems and occasionally at base of branches on the apophysis of the hydrocladium. *Gonothecae* mature, irregularly ovate, flattened distally or slightly flattened on one side, aperture closed by a thin membrane. Only female gono-

- Figs 20–22. *Salucia farquhari* (Bale). Fig. 20.—Part of stem. Fig. 21.—Stem internodes, enlarged. Fig. 22.—Single hydrotheca, anterior view.
Figs 23, 24. *Sertularella robusta* Coughtrey. Fig. 23.—“Long internode” form with large hydrothecae and smooth thecal walls. Fig. 24.—“Short internode” form, showing smaller hydrothecae with undulated walls.
Fig. 25. *Amphisbetia minima* var. *intermedia* Bale. Aberrant stem with both “*pumiloides*” (proximal part of stem) and “*intermedia*” (distal) hydrothecae.
Figs 26, 27. *Amphisbetia avia* n.sp. Holotype. Fig. 26.—Stem with female gonophore. Fig. 27.—Stem internodes, enlarged.

phores present, spherical, half filling gonothecal cavity, packed with mature ova surrounded by a thin granular blastostyle.

Remarks: Only one small colony of *H. elegans* was found growing in a relatively exposed situation.

Mature gonophores of *H. elegans* have not previously been described.

Antennella campanuliformis (Mulder & Trebilcock, 1909). Watson, 1973: 182, figs 43, 44.

Plumularia campanuliformis Mulder & Trebilcock, 1909: 31, pl. 1, figs 6, 9, 10; 1910: 115.

Record: Satellite I., on *Lenormandia marginata* and other red algae; no depth recorded.

Material: Luxuriant infertile colonies. Erect stems to 8 mm high. Colour, trophosome pinkish-yellow, stolons dark brown.

Remarks: This material conforms reasonably well with the description of Mulder & Trebilcock (1909). However, the hydrothecae are slightly more campanulate and delicate, with no thickening of the abcauline thecal wall as in specimens described from Pearson I. (Watson 1973).

The hydroid was found on one side only of the algal fronds.

This is the first record of *A. campanuliformis* from Tasmania. Other localities: Victoria; S. Aust.

Pycnotheca mirabilis (Allman, 1883) var. *mirabilis* Stechow, 1925: 241, Ralph, 1961b: 50, fig. 7a, b.

FIG. 28

Pycnotheca mirabilis (Allman, 1883). Hodgson, 1950: 50, figs 81, 82.

Diplocheilus mirabilis Allman, 1883: 49, pl. 8, figs 4-7.

Kirchenpaueria mirabilis (Allman, 1883). Bale, 1894: 109, pl. 6, figs 4-7. Briggs, 1915: 308. Blackburn, 1942: 106.

Records: Satellite I., 9 m deep; Adventure Bay, 10-22 m deep, on red algae.

Material: Fertile stems to 5 cm high. Stems monosiphonic, arising singly from hydrorhiza, lower stems devoid of hydrocladia. Gonothecae large, adnate to lower stem, hydrorhiza, or algae. Perisarc very thick, strongly ridged with up to 9 ridges, more prominent on abcauline side. Colour of gonotheca, deep red brown. Gonophores, female.

Remarks: It is difficult to distinguish between infertile stems of *P. mirabilis* and *P. producta* Bale, 1881. Examination of fertile material of both species in the Bale collection (NMV),

shows that the Bruny I. specimens correspond closely to a microslide of *P. mirabilis* from Bass Strait. Gonothecae of *P. producta* collected at Port Jackson, in 1886, are smaller (1.56-1.86 mm long, 0.75-0.84 mm wide), have a thinner perisarc, and are only faintly undulating. These are similar to Hodgson's (1950) figure and dimensions of "*P. mirabilis*". Ralph (1961a) noted the discrepancy between Hodgson's description, figures, and the actual dimensions of the gonotheca of *P. mirabilis* and suggested that it may represent a new varietal form of *P. producta*. It seems more likely, however, that the numbers of the two figures of the gonothecae of *P. producta* and *P. mirabilis* have been confused in Hodgson's paper.

Halopteris campanula var. *campanula* (Busk, 1852). Ralph, 1961b: 47. Watson, 1973: 184.

Plumularia campanula Busk, 1852: 401. Bale, 1884: 124, pl. 10, fig. 5; 1913: 133. Hodgson, 1950: 40.

Record: Satellite I., 14 m deep, under ledge.

Material: One infertile colony. Stems to 2.5 cm long, sparingly branched, lax. Colour, yellow.

Remarks: *H. campanula* var. *campanula* is represented in this collection by only one sparse epilithic colony, which was growing in reduced light in a crevice.

Plumularia filicaulis Kirchenpauer, 1876: 28, pl. 5, fig. 6. Bale, 1884: 134, pl. 11, figs 6, 7, pl. 19, figs 41, 42. Léloup, 1934: 4. Hodgson, 1950: 42, fig. 72. Millard, 1958: 209, fig. 13D. E. Shepherd & Watson, 1970: 140.

Record: Adventure Bay, 10-22 m deep, on red algae.

Material: Luxuriant infertile colonies. *Hydrorhiza* pegged, forming a reticular network on the algal frond. Stems short, simple and pinnate on the one colony. Simple stems to 2 mm, pinnate stems to 4 mm high.

Remarks: *P. filicaulis* is a common epiphyte on several species of red algae (Shepherd & Watson 1970).

Plumularia hyalina Bale, 1881: 41, pl. 15, fig. 9; 1884: 141, pl. 12, figs 4, 5. Ralph, 1961b: 41.

FIG. 29

Record: Fluted Cape, 16 m deep, on a red alga.

Material: Abundant, sparingly fertile colonies. Stems to 3 mm long, stems and hydrocladial

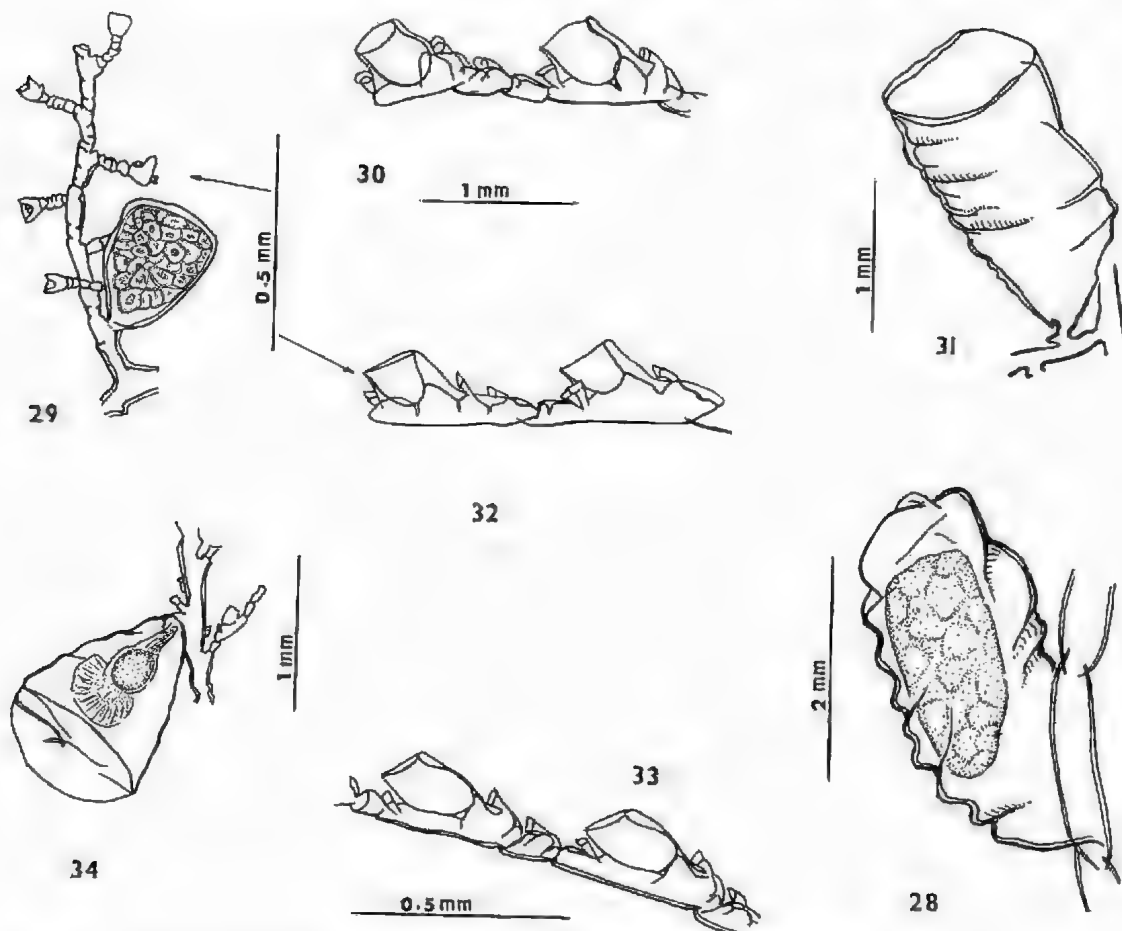


Fig. 28. *Pycnotheca mirabilis* var. *mirabilis* (Allman). Gonotheca with heavily ridged perisarc and female gonophore.
 Fig. 29. *Plumularia hyalina* Bale. Stem with ripe female gonophore.
 Figs 30, 31. *Plumularia angusta* Stechow. Fig. 30.—Part of hydrocladium. Fig. 31.—Gonotheca.
 Fig. 32. *Plumularia crateriformis* Stechow. Part of hydrocladium.
 Figs 33, 34. *Plumularia wilsoni* Bale. Fig. 33.—Part of hydrocladium. Fig. 34.—Gonotheca, showing downwardly directed growth habit.

internodes strongly ridged, hydrocladia with one terminal hydrotheca, *Gonothecae* large, top-shaped, greatest width distally, 0.7 mm wide, 0.9 mm long; gonophores mature, female only; completely filling gonothechal cavity. Colour, stems white to yellow; gonophores bright yellow.

Remarks: This is the first record of mature *P. hyalina* in Australian waters. Ralph (1961b) described much longer (1.3–1.7 mm) and slightly narrow (0.5–0.65 mm) gonothecae for her mature specimens from New Zealand. Judging by this considerable difference in size of gonothecae, it seems that an as yet undocumented range of geographic variants of *P. hyalina* may exist.

Some stems of the material from Bruny I. have a well developed "stolonic plate" identical with that described for *Plumularia epibractea* Watson, from Pearson I.

This is a new record for Tasmania. Other localities: Vic.; S. Aust.; New Zealand.

Plumularia angusta Stechow, 1923b: 226. Blackburn, 1942: 108.

FIGS 30, 31

Plumularia setaceoides vars a, b, d, Mulder & Trebilcock, 1910: 117, pl. 2, fig. 9, pl. 3; figs 3, 6.

Records: Penguin I., 15 m deep, on *Macrocystis* holdfast and sponge; Adventure Bay, on *Macrocystis* holdfasts and the brown alga *Myriodesma quercifolium*.

Material: Abundant fertile stems to 1 cm long. *Hydrothecae* pitcher-shaped, but variable, some with a pronounced concavity of the adcauline wall and a constriction behind margin, others with a thickening of the abcauline wall. Colour, straw-coloured, gonothecae bright orange.

Remarks: The hydrothecae are very variable in shape even on the one hydrocladium, the thecal walls ranging from pitcher-shaped to almost straight, often closely approaching the shape of the hydrotheca of *P. setaceoides*.

Plumularia crateriformis Stechow, 1923b: 227.
FIG. 32

Plumularia setaceoides var. *crateriformis*
Mulder & Trebilcock, 1910: 118, pl. 3, figs 8,
8a; 1915: 51, pl. 7, figs 3, 3a.

Record: Adventure Bay, 4–6 m, on the brown alga *Xiphophora gladiata*.

Material: Infertile stems to 1 cm long.

Remarks on *P. angusta* and *P. crateriformis*: Stechow (1923b, pp. 226, 227) raised Mulder & Trebilcock's varieties of *P. setaceoides* (the unnamed vars a, b, d, and var. *crateriformis*) to specific rank, his distinction between the two species resting largely on the shape of the hydrotheca, a character of considerable variability in this group and thus of doubtful diagnostic value. The material from Bruny I., although showing some intergradation, can, however, be fairly readily assigned to one or other of these two species.

This, together with the fact that the two species occur together in the one locality, although at different depths and on different algal substrates (and one, *P. angusta*, was fertile, while *P. crateriformis* was not) indicates that these are valid, although closely related species radiating from the central *P. setaceoides* stock.

Neither *P. angusta* and *P. crateriformis* have previously been recorded from Tasmania. They may have been confused with *P. setaceoides*. *P. angusta* is known from Victoria and S. Aust.; *P. crateriformis* from Victoria.

Plumularia wilsoni Bale, 1926: 21. Ralph,
1961b: 31, figs 2, 3,

FIGS 33, 34

Plumularia delicatula Bale, 1881: 28, pl. 15,
fig. 2; 1884: 137, pl. 11, fig. 5, Mulder &
Trebilcock, 1910: 115, pl. 2, fig. 2.

Records: Penguin I.; Adventure Bay; Satellite I., 3 m deep, on sponge.

Material: Sparse fertile stems to 2 cm long. *Gonothecae* top-shaped, 1 or 2 arising on a

very short pedicel from proximal part of stem, distal end directed downwards towards substrate. Perisarc delicate, very faintly undulated, no operculum. Gonophores—male.

Remarks: The trophosome of the Bruny I. specimens corresponds very closely with Bale's material of *P. wilsoni* from Griffiths Point, Victoria. The submarginal constriction behind the hydrothecae of the present material is rather variable, being more pronounced in some hydrothecae than in others even on the same hydrocladium. The hydrothecae with a shallow constriction closely approach those forms of *P. setaceoides* with more recumbent hydrothecae.

The gonothecae of the Bruny I. specimens are identical with those of Mulder & Trebilcock's (1910) microslide from which they described the gonotheca of *P. wilsoni*. Their figure is, however, misleading, as the walls of the figured specimens, like those of the present material, are only faintly undulated, not heavily ridged, as may be inferred from their figure.

A new record for Tasmania. Other localities: Victoria; New Zealand.

Aglaophenia plumosa Bale, 1881: 25, pl. 14,
fig. 6; 1884: 153, pl. 14, fig. 5, pl. 17,
fig. 12; 1924: 257. Blackburn, 1942: 110.
Hodgson, 1950: 56, fig. 87. Shepherd &
Watson, 1970: 140.

Record: Fluted Cape, 20 m deep, on sponge.

Material: Rare infertile colonies. Stems to 1 cm long.

Remarks: This is the robust form of *A. plumosa* with short hydrocladial and stem internodes. Hodgson notes that his material collected from *Macrocystis* and drift had shorter stems (i.e. the short internode form) than those stems collected from the seagrass *Zostera*, which grows in sheltered waters.

Thecocarpus divaricatus var. *typica* (Busk,
1852). Shepherd & Watson, 1970: 140.

Aglaophenia divaricata Busk, 1852: 398.

Records: Adventure Bay, 1–10 m deep, on horizontal faces among holdfasts of brown alga *Phyllospora comosa*; 10–22 m deep, epilithic in sheltered situations.

Material: Stems infertile, to 10 cm in height, branched. Cauline nematothecae similar in shape to those of *T. divaricatus* var. *cystifera*, but much smaller. *Hydrocladia* close-set, hydrothecae crowded on hydrocladium, no oblique intranodal septa on thecate hydrocladial internode. Colour, dark brown.

Thecocarpos divaricatus* (Busk) var. *briggsi

Bale, 1926: 22, fig. 5, Watson, 1973: 194.
Record: Satellite I., on the red alga *Thamno-*
clonium dichotomum. No depth recorded.

Material: Straggling, irregularly branched,
 stems to 15 cm long. Colonies infertile. Colour,
 black.

This is the first record of var. *briggsi* from
 Tasmanian waters. Other localities, Port
 Jackson, N.S.W. (Bale); Pearson I., S. Aust.
 (Watson).

Remarks on the varieties of T. divaricatus at
Bruny Island: The two varieties of *T. divari-*
catus recorded at Bruny I. are easily distinguish-
 able by the presence of an intranodal ridge in
 the hydrocladium of var. *briggsi*, as well as in
 differences in habit and substrate preferences
 of each.

The var. *briggsi* was found only in sheltered
 reefs near Satellite I., in the D'Entrecasteaux
 Channel, where it was a common epiphyte on
Thamnoclonium. The more robust var. *typica*
 occurred on rock faces and as a common epi-
 phyte on *Phyllospora* holdfasts in situations of
 moderate exposure to surge.

Although showing affinities with var. *cysti-*
fera, the latter form does not display the dis-
 tinctive planar growth habit recorded for this
 variety (Watson 1973), nor the enlarged
 cauline nematothecae. In microstructures it
 most closely resembles a fragment of Busk's
 type of *Aglaophenia divaricata* from Bass Strait
 (NMV collection) and is thus recognized here
 as var. *typica*.

T. divaricatus is a common and variable
 species of the southern Australian coast.
 Further study is necessary to elucidate the sys-
 tematic status and ecological relationships of
 the varieties of this species.

***Halicornaria longirostris* (Kirchenpauer, 1872).**

Bale, 1884: 181, pl. 13, fig. 7, pl. 16,
 fig. 3, pl. 19, fig. 30, Hodgson, 1950: 51
 fig. 83, Watson, 1973: 197.

Records: Penguin I., 10–20 m deep, on *Theca-*
carpus divaricatus; Adventure Bay, 10–20 m
 deep, on red algae and epilithic on vertical
 faces; Satellite I., 12 m deep, on *T. divaricatus*
 var. *briggsi*.

Material: Luxuriant colonies; stems 3–8 cm
 long, unbranched, infertile.

Remarks: The material from Bruny I. displays
 the same range in substrate as already noted for
H. longirostris at Pearson I. (Watson 1973).
 Epilithic colonies from faces exposed to surge
 have the longest and most robust stems, while

epizoic colonies on *T. divaricatus* var. *briggsi*
 from both Penguin I. and Satellite I. (i.e. from
 protected and relatively rough-water situations)
 had somewhat shorter, lax stems, given off
 singly from a stolon creeping on the stem of
 the hydroid host. The cauline internodes of
 these latter stems are long, with distant hydro-
 cladia, the hydrocladia themselves having long
 internodes, and the mesial nematotheca extends
 well over the mouth of the hydrotheca. Rare
 epiphytic colonies on red algae at Adventure
 Bay had the shortest stems. There were no
 discernible differences in microstructures be-
 tween these three ecomorphs. Briggs (1915)
 mentions that his specimens from Storm Bay
 were "86 mm in height (and) were found asso-
 ciated with *Aglaophenia divaricata*". Hodgson
 (1950) did not record the substrate of his
 material from Blackman's Bay in the Derwent
 Estuary.

Discussion***Ecology***

Campanulariidae were recorded from all
 depths, being epiphytic on red algae growing
 mostly in sheltered places. One exception, *Sili-*
cularia rosea, was associated with the brown
 algae *Scytothalla dorycarpa* and *Sulcococcus*
axillaris in situations of moderate water move-
 ment.

The only representative of the Lafoeidae,
Hebella furax, provisionally recorded for the
 first time in Australian waters, is a small form
 epizoic on the stems of *Thecocarpus divari-*
catus var. *briggsi* Bale. The majority of species
 of the Lafoeidae known from Tasmanian and
 mainland Australian waters are larger forms
 from the deeper continental shelf, hence are
 unlikely to be found in a shallow water collec-
 tion such as the present one from Bruny I.

With the exception of *Phylactotheca armata*
 and *Halecium* sp., all haleciid species in the
 collection are epizoic forms. *Halecium delicatu-*
lum Coughtrey [*H. flexile* of Hodgson (1950)]
 is one of the most abundant hydroids at Bruny
 I., the luxuriant orange-yellow colonies growing
 on the crustose bryozoan *Membrinopora mem-*
brinacea epiphytic on old stipes of the large
 kelp *Macrocystis pyrifera*. The two species
 newly described, *Halecium brunensis* and
H. luteum, as well as *H. beanii*, are of cryptic
 habit, the two new species growing on sponge,
 bryozoa, and rock in crevices, while *H. beanii*
 occurs on the underside of the large plate-like
 alga *Sonderophycus australis*. While fertile
 colonies of *Phylactotheca armata* were recorded
 abundantly at all rough-water sites, they in fact

also occupied a relatively sheltered microhabitat among the holdfasts of the brown alga *Phyllospora comosa*.

Remarkably few species of Sertulariidae were recorded. Of greatest interest is the first record of *Salacia farquhari* (Bale) outside New Zealand waters (see further discussion below). *S. farquhari* was, however, rare at Bruny I. *Sertularia acuta* Stechow, while one of the most abundant epiphytes in the collection, was associated only with red algae, and not with *Macrocytis* as were Hodgson's specimens. Hodgson (1950) also recorded very abundant colonies of *Amphisbetia operculata* on old scallop shells from the D'Entrecasteaux Channel. Careful search in the area of the D'Entrecasteaux Channel covered in this survey produced only one attenuated colony. Although *A. operculata* is known to display strong seasonal growth, some of the rootstock and putts of the colonies usually persist from one season to another (pers. observ.). The virtual absence of this species from a former habitat may be explained by permanent changes in the ecosystem brought about by invasion of the gastropod *Maoricolpus roseus*, following the collapse of the scallop dredging industry. Probably the shell of *M. roseus* does not offer an attractive substrate to the larvae of *A. operculata*.

Of particular interest is the occurrence in one locality of three species, *Plumularia angusta*, *P. crateriformis* and *P. wilsoni*, all of which are known from Victoria. *P. angusta* is also recorded from South Australia (Blackburn 1942) and *P. wilsoni* from New Zealand (Ralph 1961b), where it is, however, rare. These species are closely related to one another and to *Plumularia setaceoides* Bale, endemic to southern Australian and New Zealand waters, from which central stock they may have radiated.

None of the larger Plumularians were of common occurrence. *Halicornopsis elegans* and *Thecocarpius divaricatus* var. *typica* were found in sheltered situations. The association of *T. divaricatus* var. *briggsi* with a bluish coloured sponge investing the warty surface of the alga *Thamnoclonium dichotomum* has not previously been observed. *Halicornaria longirostris* was moderately abundant at all sampling sites, the three ecomorphs of this species displaying an identical choice of substrate with that reported from Pearson I. (Watson 1973).

Zoogeography

The Bruny I. material, although collected from a restricted locality, yielded 11 new

records for Tasmania, including 3 new records for Australian waters. Seven of these species are already known from the Victorian coastline of Bass Strait, so would be expected to occur among the Tasmanian fauna. *Thecocarpius divaricatus* var. *briggsi*, now known from N.S.W. (Bale 1926), Tasmania and South Australia (Watson 1973) has not yet been recorded from Victoria.

Of the 3 new records for Australia, *Halecium beani* is cosmopolitan, *Hebella furax* is known only from South Africa, while *Salacia farquhari* is a New Zealand species recorded only from the South Island, where it does not, however, occur north of 43°S. The absence of *S. farquhari* from mainland Australian waters may thus be attributable to this southern distribution, as Bruny I. also lies close to 43°S.

The profound influence of the East Australia Current and the West Wind Drift in the dispersal of species and the biological and zoogeographic relationships of the trans-Tasman hydroid fauna have been discussed at length by Ralph (1961c). In this regard, three species recorded from Bruny I. are of considerable interest. These are the two haleciids newly described, and the occurrence of *S. farquhari*. *Halecium hynniensis* bears a strong resemblance to *H. lenticularis*, a species known from the South Island of New Zealand and Cook Strait, while *H. luteum* displays close affinities with *H. corrugatissimum*, a rare species recorded from both North and South Islands. The striking similarities in stem morphology between the members of these two pairs, as well as the gross differences in habit (both Australian species are polysiphonic, and the colonies are larger), strongly suggests active progress of speciation from a common stock in addition to dispersal across the Tasman Sea.

Acknowledgments

I am indebted to Professor H. B. S. Womersley, Botany Department, University of Adelaide, for identification of algae; to my diving companions, S. A. Shepherd, R. Baldoek and N. Coleman, for assistance in the field and to Miss Rhylis Plant for some of the drawings. I gratefully acknowledge financial support in the form of a research grant from the Trustees of the C.S.I.R.O. Science and Industry Endowment Fund and a field research grant from the Royal Society of South Australia which partly met the costs of this study.

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SHOOT AND FOLIAGE PRODUCTION OF FIVE SHRUB SPECIES OF *ACACIA* AND *HAKEA* IN A DRY SCLEROPHYLL FOREST

BY J. R. MACONOCHIE*

Summary

MACONOCHIE, J. R. (1975) .-Shoot and foliage production of five shrub species of *Acacia* and *Hakea* in a dry sclerophyll forest. *Trans. R. Soc. S. Aust.* **99**(4), 177-181, 30 November, 1975.

An examination has shown that shoot growth of *Acacia myrtifolia*, *A. pycnantha*, *Hakea rostrata*, *H. rugosa* and *H. ulicina* is distinctly seasonal. Growth commenced in spring, finished by mid-summer and was preceded by flowering.

The maximum rates of loss of foliage occurred towards the cessation of active shoot growth and both mature and juvenile foliage was lost. Measurements of size of shoots of the three species of *Hakea* over a series of years suggested that the available soil moisture during the growth period was the controlling factor for shoot size. It is further suggested that the growth habit of these three species is reflected in the pattern and size of new shoots along a parent shoot. *H. ulicina*, the species which showed a tendency toward apical dominance is an erect, several stemmed shrub, whereas *H. rostrata* and *H. rugosa* are rounded spreading shrubs.

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Introduction

This study on shoot production of the five temperate shrubs, *Acacia myrtifolia* (Sm.) Willd., *A. pycnantha* Benth., *Hakea rostrata* F. Muell. ex Meisn., *H. rugosa* R. Br. and *H. ulicina* R. Br., was part of a project in which shoot growth was measured on other shrubs from the arid and semi-arid areas of South Australia (Maconochie & Lange 1970, Maconochie 1973), to obtain basic phenological data in a range of habitats.

Study Site and Methods

This study was carried out on the boundary of the Para Wirra Reserve in the Mt Lofty Ranges, South Australia from April 1965 until January 1967. The occurrence and size of new shoots produced on about 120 tagged shoots of each species of *Hakea* and *A. pycnantha*, and of 25 tagged shoots on two bushes of *A. myrtifolia*, were recorded monthly. The technique has been described previously (Maconochie & Lange 1970).

From 1965 until 1971, samples of shoots were collected at the end of the growing season from the three *Hakea* species and data recorded on size and position of new shoots.

These data for axillary and terminal shoots were separated and the annual mean shoot sizes compared by analysis of variance.

Climatic data were supplied by the Australian Bureau of Meteorology.

Results

Qualitative Aspects

The percentage cumulative gains and losses of foliage for *A. pycnantha* and *A. myrtifolia* are presented in Fig. 1. *A. myrtifolia* did not produce any new shoots in the first year of the study but the burst of growth during the second year was in phase with that of *A. pycnantha*. The "stepped" effect displayed by *A. pycnantha* was also produced by *H. rostrata*, *H. rugosa* and *H. ulicina*. New shoot growth was distinctly seasonal.

Figure 2 presents the relative rates of gain and loss for the five species. Climatic data are presented in Fig. 3; soil moisture values were taken from Martin & Specht (1962).

Shoot growth reached a peak during October when daily temperatures were increasing and soil moisture was available (Figs 2 and 3). In both 1965 and 1966, flowering, which commenced in early August and finished by the

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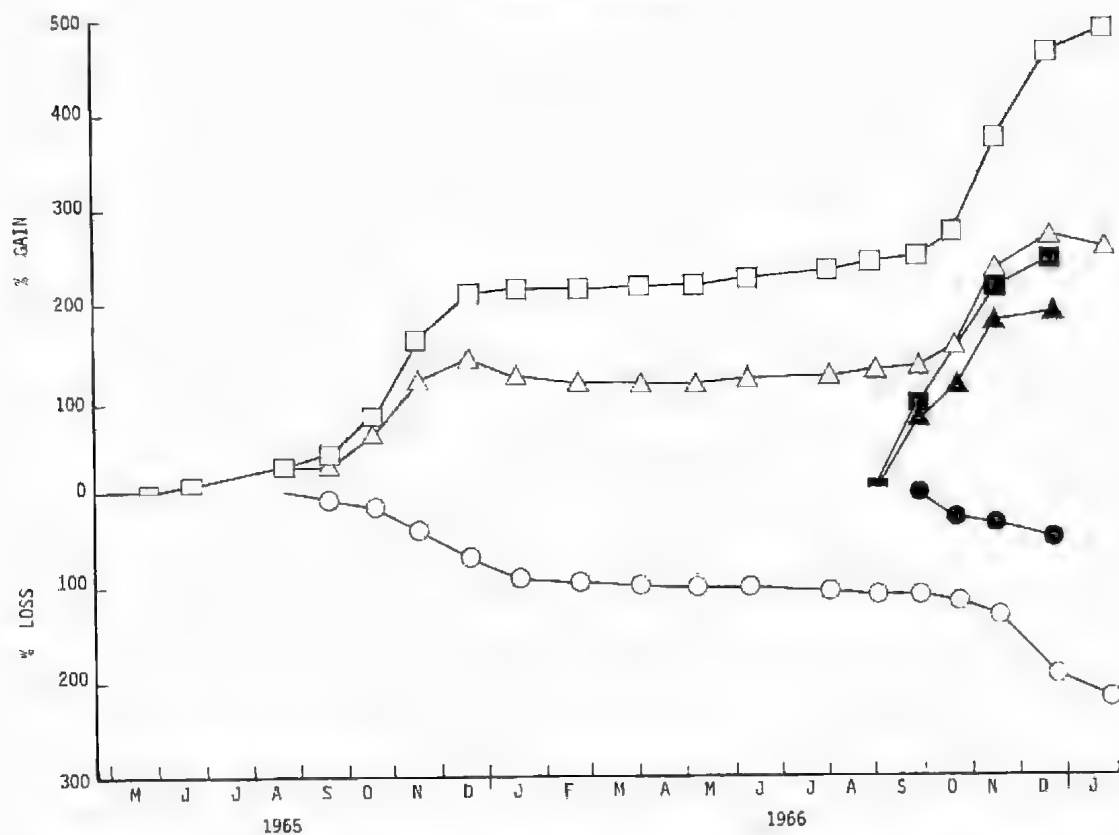


Fig. 1. The percentage cumulative leaf gain and loss of *A. pycnantha* (□, total new positions; Δ, leaves; ○, scars), and *A. myrtifolia* (■, new positions; ▲, leaves; ●, scars).

end of September, preceded shoot growth. Immature flower buds on the *Acacia* species were observed to develop as early as January. Both axillary and terminal flower and shoot buds on the *Hakea* species were enclosed in bracts and these buds developed as the new leaves matured. This observation suggested that the size of new shoots for the next season may be predetermined by conditions at the time of bud development.

Although the *A. myrtifolia* bushes did not produce new shoots in 1965, flowering did take place.

The peaks in rates of foliage loss coincided with or immediately followed the peaks of production, with loss comprising both mature senescing and soft immature foliage. Some further loss was caused during a severe wind and hail storm in December 1966 in which trees and branches were felled, and also by bird pruning during July-August 1966. Parrots were observed pruning all the trees and tall shrubs, apparently at random, in the area and

in some cases clipping off branches up to 5 mm thick.

Some losses of *H. ulicina* and *H. rostrata* during January-February 1966 were a result of the death of several plants. These bushes were not examined for cause of death, but since rainfall in 1965 was 223 mm below average it is probable that localised drought during summer was the most likely cause of death.

Generally once new foliage had matured, the rate of leaf loss on the *Hakea* species declined to almost zero. The needle-like, rigid, sclerophyllous leaves of these species are obviously more resistant to physical damage than the leaves of the more mesomorphic species of the community.

Quantitative Aspects

The mean number of leaves per shoot for each species and for the years 1965 to 1971 inclusive are presented in Table 1. Analysis of these data showed that for some years

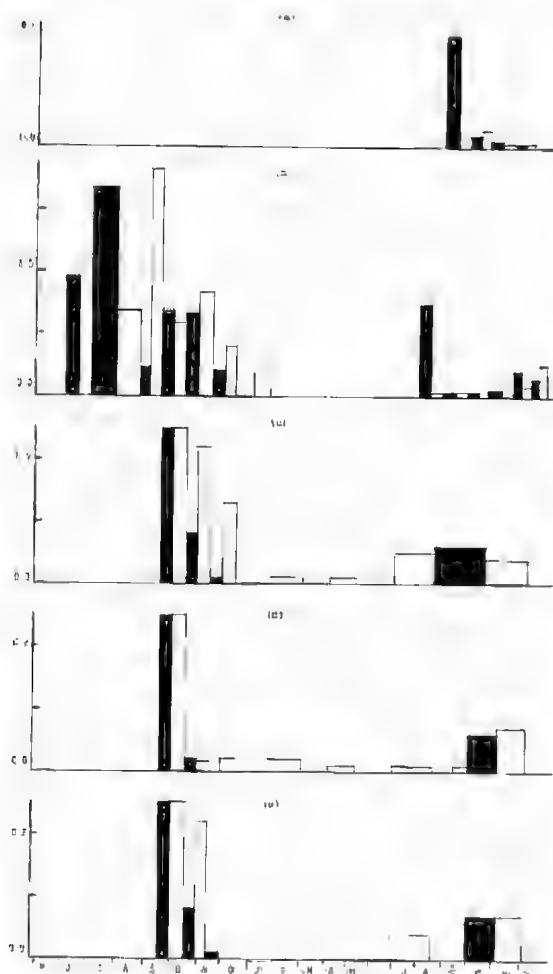


Fig. 2. The relative rates of gain (block) and loss of foliage of (a) *A. myrtifolia*, (b) *A. pycnantha*, (c) *H. ulicina*, (d) *H. rostrata*, and (e) *H. rugosa*, for the years 1965 and 1966.

there was a significant difference between the sizes of shoots produced in successive years. In other years, the variation in shoot size was so large that no significance could be attached to the differences.

A set of correlation coefficients (r) and regression equations were computed between total rainfall (\bar{x}) for the period September to November and the mean shoot sizes (\bar{y}) for successive years during which there were significant differences ($P < 0.05$) between the means. This rainfall period was selected because it was the time of active growth.

H. ulicina—axillary shoots

$$r = +0.74 \quad 0.10 > P > 0.05$$

$$y = 5.0 + 0.014x$$

H. rostrata—terminal and axillary shoots

$$r = +0.52 \quad P > 0.10$$

$$y = 5.1 + 0.008x$$

H. rugosa—terminal and axillary shoots

$$r = +0.83 \quad .05 > P > .02$$

$$y = 4.1 + 0.029x$$

H. rugosa was the only species showing an acceptably significant correlation between mean shoot size and rainfall during the growing season.

Calculation of the correlation coefficient between the mean shoot size and rainfall period September–November of the preceding year gave the following: *H. ulicina*—0.65, *H. rostrata*—0.07, and *H. rugosa*—0.55.

Analysis of the data for 1966 on the relative positions of shoots showed that there were no significant differences in shoot sizes between pairs of positions distal to the apex (Table 2) except for *H. ulicina*. In this species there was a significant difference ($P < 0.05$) between the mean of the terminal and that of the first axillary position. Further analysis showed significant differences ($P < 0.05$) between terminal and axillary positions two and three. It would appear, therefore, that *H. ulicina* is the only one of these three species which has a tendency towards apical dominance.

Discussion

Cambage (1918, 1927) measured the height growth of *A. pycnantha* at Sydney Botanic Gardens and his study showed the normal pattern of rapid growth during the juvenile stage followed by a decreasing rate as the plant matured. The plants studied at Para Wirra were mature and the rates of growth as reflected in both Figs 1 and 2 were of a "steady state" nature, as occurs at the plateau of the sigmoid growth curve.

Martin & Specht (1962) measured the moisture relationships in a dry sclerophyll forest, of which these species are shrub components. Their studies showed that the more mesic community of this vegetation type had a higher index of evapotranspiration and could be subjected to a drought period during the mid-summer. The three species of *Hakea* and two *Acacia* species all show a distinct seasonality of shoot growth with a cessation occurring in mid-summer probably during the drought period or when soil moisture is only sufficient to maintain a dormant growth phase.

The negative correlation between mean shoot size and soil moisture (as reflected by

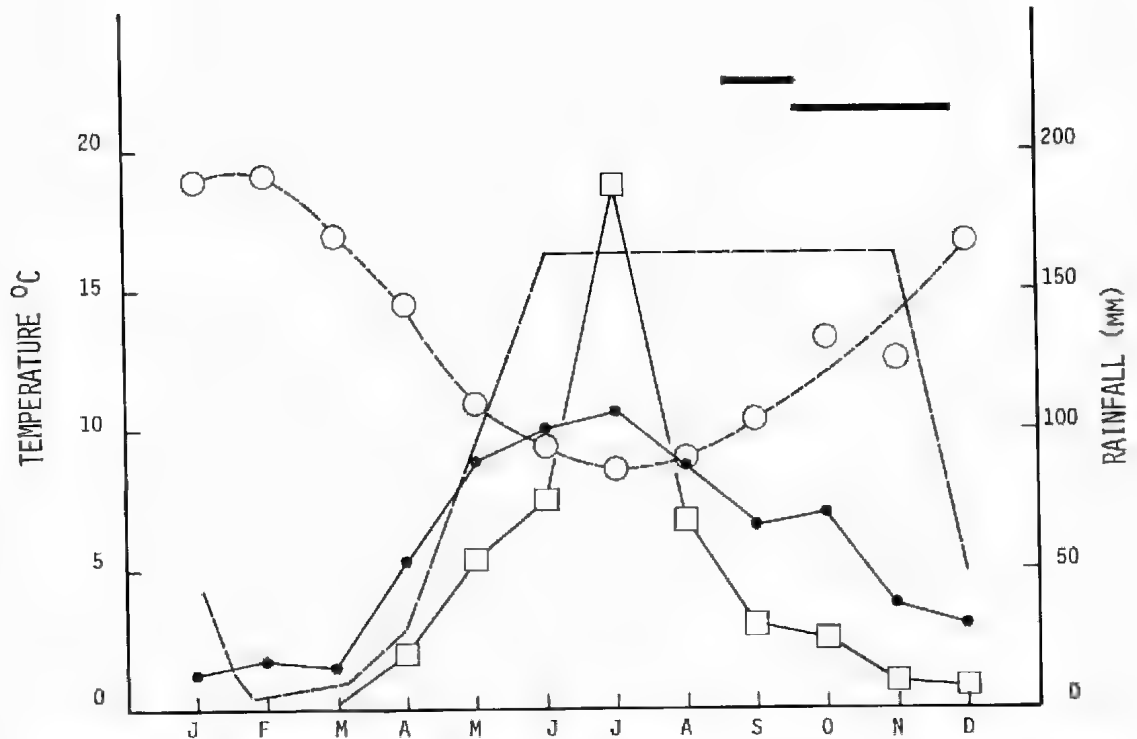


Fig. 3. Climatic data of Parra Wirra study site; soil moisture ex Martin & Specht (1962), other data means for 1965-1970. —, soil moisture; ○, mean temperature; —, rainfall; □, potential evapotranspiration (P/E 0.75); —, florescence and duration of active growth.

TABLE 1
Mean number of leaves per shoot for seasons 1965 to 1971

| Species | Shoot Posn. | 1965 | 1966 | 1967 | Year 1968 | 1969 | 1970 | 1971 |
|-----------------------|-------------|------|------|------|-----------|------|------|------|
| <i>Hakea ulicina</i> | Total | 7.4* | 8.1* | 8.2 | 8.7 | 9.2 | 9.4 | 9.8 |
| | Terminal | 9.6 | 10.2 | 9.4* | 9.4 | 10.9 | 10.6 | 11.2 |
| | Axillary | 5.9† | 7.1† | 4.9‡ | 8.1* | 6.7† | 8.9 | 8.4 |
| <i>Hakea rostrata</i> | Total | 6.4‡ | 5.8† | 5.2 | 5.4‡ | 6.5 | 6.7‡ | 9.0 |
| | Terminal | 6.1 | 6.1 | 5.7 | 5.4‡ | 7.0 | 6.5‡ | 10.6 |
| | Axillary | 6.5‡ | 5.7 | 5.2 | 5.4‡ | 6.4 | 6.8* | 7.5 |
| <i>Hakea rugosa</i> | Total | 7.2‡ | 9.1‡ | 4.6‡ | 8.7 | 8.4† | 9.2‡ | 13.7 |
| | Terminal | 7.3‡ | 9.4 | 8.1 | 8.8 | 8.8 | 9.5‡ | 15.9 |
| | Axillary | 6.9‡ | 9.0‡ | 4.4‡ | 8.8 | 8.3* | 8.9‡ | 12.7 |

Significant differences between mean and mean of succeeding year are indicated.

* $P < 0.05$; † $P < 0.01$; ‡ $P < .001$.

TABLE 2
Mean number of leaves per shoot for terminal and axillary positions distal from shoot tip for year 1966

| Relative Position | Term. | AX ₁ | AX ₂ | AX ₃ | AX ₄ | AX ₅ | AX ₆ | AX ₇ | AX ₈ |
|--------------------|-------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| <i>H. ulicina</i> | 10.9* | 7.8 | 7.5 | 7.2 | 7.6 | 7.4 | 6.6 | 7.6 | 5.6 |
| <i>H. rostrata</i> | 6.2 | 6.0 | 5.3 | 5.6 | 5.3 | 5.3 | | | |
| <i>H. rugosa</i> | 9.3 | 8.6 | 9.6 | 10.2 | 10.3 | 8.2 | | | |

* Indicates significant difference ($.05 > P > .01$) between mean and that of succeeding position.

rainfall) during the growing period of the previous year suggests that shoot size in the following year is not necessarily determined at the bud formation stage. Rather these results suggest that shoot size is more likely to be determined by the soil moisture during the period of active growth.

The time of shoot growth for these species contrasts with that of heath studies of Specht (1957), Specht & Rayson (1957) and Groves (1965), who recorded that the shoot growth commenced in December when soil moisture was decreasing. Specht (1957) showed that drought conditions occurred in both December and January. Groves (1965) noted that shoot-growth continued throughout the summer of his study period; however a recharge of soil moisture from a mid-summer rain was recorded.

Maconochie & Lange (1970) and Maconochie (1973) have reported the seasonality of shoot growth on *A. sowdenii*, *A. ligulata* and *A. murrayana*, and possible non-seasonal and seasonal shoot growth responses on *A. aneura* and *A. kempeana*. Wetherell (1966) recorded flushes of growth on *A. harpophylla* in Queensland during spring and summer, and during one period of early winter. *A. pycnantha*, by

contrast, actively grew only during the spring period at the study site, and although shoot growth on *A. myrtifolia* was only recorded during the second year, it appears that from this slender evidence that the shoot growth follows a seasonal pattern also.

Both *H. rostrata* and *H. rugosa* have a more spreading bushy habit than *H. ulicina* which has a tendency to be more erect. The habit of these plants is reflected in the sizes of new shoots on a parent shoot. Both *H. rostrata* and *H. rugosa* did not produce significantly smaller axillary shoots in comparison to the terminal, but the terminal shoots of *H. ulicina* were significantly larger than shoots on the three succeeding positions below the apex. This suggests a tendency towards apical dominance and thus explains the more erect habit of this species.

Acknowledgments

The author is indebted to Dr R. T. Lange, Botany Department, University of Adelaide, for his encouragement in the first part of the project. Dr R. W. Rogers, now of the University of Queensland, supplied samples during the years 1967 to 1970 and his assistance is gratefully acknowledged.

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SHORELINE SHINGLE TERRACES AND PREHISTORIC FILLINGS OF LAKE EYRE

BY J. A. DULHUNTY*

Summary

DULHUNTY, J., A. (1975).-Shoreline shingle terraces and prehistoric filling of Lake Eyre.

Trans. R. Soc. S. Aust. 99(4), 183-188, 30 November, 1975.

Investigations were carried out of (i) development of contemporary wave-built shingle terraces during the 1974 record historic filling of Lake Eyre, and (ii) old shoreline shingle terraces built by prehistoric fillings of the Recent salina to levels above that of 1974.

Evidence indicates at least three prehistoric fillings to levels of 280, 160 and 70 cm above that of the 1974 filling. No precise evidence of the ages of the prehistoric fillings was obtained, but estimates inferred from field studies suggested dates of the order of 3,000, 1,500 and 500 years before present. The "3,000" year old filling was probably the deepest during the Recent salina episode of the history of Lake Eyre. The possibility of more permanent, deeper and widespread pre-salina filling of the lake, and late Recent subsidence of its southwestern areas, was also inferred from field observations.

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Introduction

Lake Eyre consists of a large northern area—Lake Eyre North, connected by a narrow channel to a small southern area—Lake Eyre South (see 1:250,000 Topographical Sheets Noolyeana, Lake Eyre, Curdimurka). It is a salina forming the "sump" of a large internal drainage system (Bonython 1955; Mason 1955; Wopfner & Twidale 1967). Aridity and high rate of evaporation, over the greater part of the drainage area, normally prevent river water from reaching the lake. On infrequent occasions when rivers flow into it, part or whole of the lake bed is covered with water which cannot escape and must evaporate. The bed of Lake Eyre North slopes gently from north to south, and evaporation of brines in the southern bays has produced salt crusts (Dulhunty 1974; Bonython 1956).

When the lake contains water, its shores are actively eroded by wave action, producing well-defined shorelines with shelving strands or low cliffs rising abruptly from its almost flat bed. At some places, cliffs up to 10 m or more in height have been cut in soft, partly consolidated sediments. At other places shorelines lie along, or around the ends of, longi-

tudinal sand ridges rising steeply to as high as 10 m above the lake bed.

Around Babbage and Hunt Peninsulas and in Belt Bay (Fig. 1A), shores are being eroded in hard dolomite, silcrete and ferruginised siltstone (Williams 1973¹). Wave action, during periods of filling, has produced quantities of pebbles or shingle consisting largely of slightly flattened and rounded pebbles from 2–10 cm in diameter. Single strands or beaches have developed, and breaking waves have washed up across the beaches long parallel deposits of shingle. These deposits, formed during the present salina episode of the lake's geological history, as discussed later, are Recent to contemporary in age. They are wave-built; strand, shingle terraces forming ridges, terraces, ramparts and banks, closely associated with the present shoreline of the salina. For the purpose of the present paper they are referred to as "the shoreline shingle terraces of Lake Eyre salina".

Gravel deposits were observed and recorded by Williams (1973¹, 1975) on Hunt and Babbage Peninsulas and on the western side of Belt Bay. He described them as "strand gravels" and "old shoreline deposits". They

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¹ Williams, A. F. (1973).—Explanatory Notes for the LAKE EYRE 1:250,000 Sheet. S. Aust. Dept. Mines, R.B. 72/93 (unpubl.).

include the Recent shoreline shingle terraces described in this paper, and other gravel deposits, possibly at higher levels, and more remote from the present shoreline, which may be older and related to pre-Recent history of the Lake. Williams (pers. comm. 1975) also noted shoreline shingle terraces along the southern shores of Lake Eyre South, which he regards as probably similar in age and origin to those of Lake Eyre North described in this paper. He also found and examined more remote terraces up to 20 km from the present lake shore.

The filling of Lake Eyre in 1974 to the greatest depth known since European settlement, provided a unique opportunity for the study of contemporary shingle terrace development in relation to lake levels and wave action. This was undertaken to gain a better understanding of the nature and origin of the old shoreline terraces and enable interpretation of their significance regarding the maximum depth to which the lake had been filled during its role as the salina of the present internal drainage system, and the time since it was filled to, or above, the level of the 1974 filling. Such investigations and results, recorded in this paper, are confined to the significance only of terraces along present shorelines, and do not represent a comprehensive study of all shingle deposits and their regional distribution around Lake Eyre.

Investigation of shingle terraces

Contemporary mean lake level

During the latter half of 1974, water level around the shores of the lake provided a horizontal datum, at any one time within certain limits of variation, which was used extensively in determining levels of shoreline shingle terraces in relation to each other and to mean lake level. Short term variations in water level were caused by wind tides, currents and possibly other factors. Wind tides were most pronounced on windward shores where water level rose and fell, within a maximum range of about 45 cm, very quickly with rise and fall of wind velocity and wave height. When wind dropped, wave action usually ceased and water level fell to "normal" within 5 to 6 hours. "Normal" water level or the level free of wind effects during periods of calm, varied as a result of other factors within a range of about 20 cm. In view of this it was assumed, for the purpose of the present investigation, that

water level at any point along the shore, measured after a calm period of not less than 6 hours, could be regarded as mean lake level plus or minus 10 cm.

Contemporary shingle terraces

Studies of shingle terrace development associated with the 1974 filling of Lake Eyre were carried out in August of that year. Mean lake level reached its maximum during May. It rose by only about 20 cm during April, remaining steady during May and fell by about 20 cm during June and July. Therefore, the shingle terraces studied in August had been built over a period of four months during which mean lake level rose and fell through only about 20 cm.

Well-defined shingle terraces were built along all shelving shores with shingle beaches around Hunt and Babbage Peninsulas, and in Belt Bay. They were built during periods of strong wind, by waves breaking and washing shingle up across the beaches to form terraces above mean lake level. It was evident that shingle moved slowly up the beaches as the lake filled, then formed into fully-developed terraces during the maximum mean lake level period, and finally remained stranded when water fell, providing evidence of the highest level reached.

The 1974 contemporary shingle terraces varied in width up to 500 cm, and in depth or thickness up to 150 cm above pre-existing beach material. The height of their tops above maximum mean lake level attained during their development, reached a general maximum of 90 cm (± 5 cm) on exposed shores. On sheltered shores, terrace tops were lower. All the terraces formed at any one time, at a given mean lake level, could be regarded as a group, although the height of their tops above mean lake level varied from place to place depending on degree of exposure to wave action. It was found that the general level of the tops of the highest terraces, on exposed shores, was a uniform feature of a group, and the most significant feature in determination, after the water level had fallen, of the mean lake level at which they had formed. Therefore, it was concluded that the maximum mean lake level of any past filling would be very close to 90 cm below the general level of the original tops of the highest shingle terraces produced during that filling.

Greater depths of water during prehistoric fillings are not likely to have produced waves

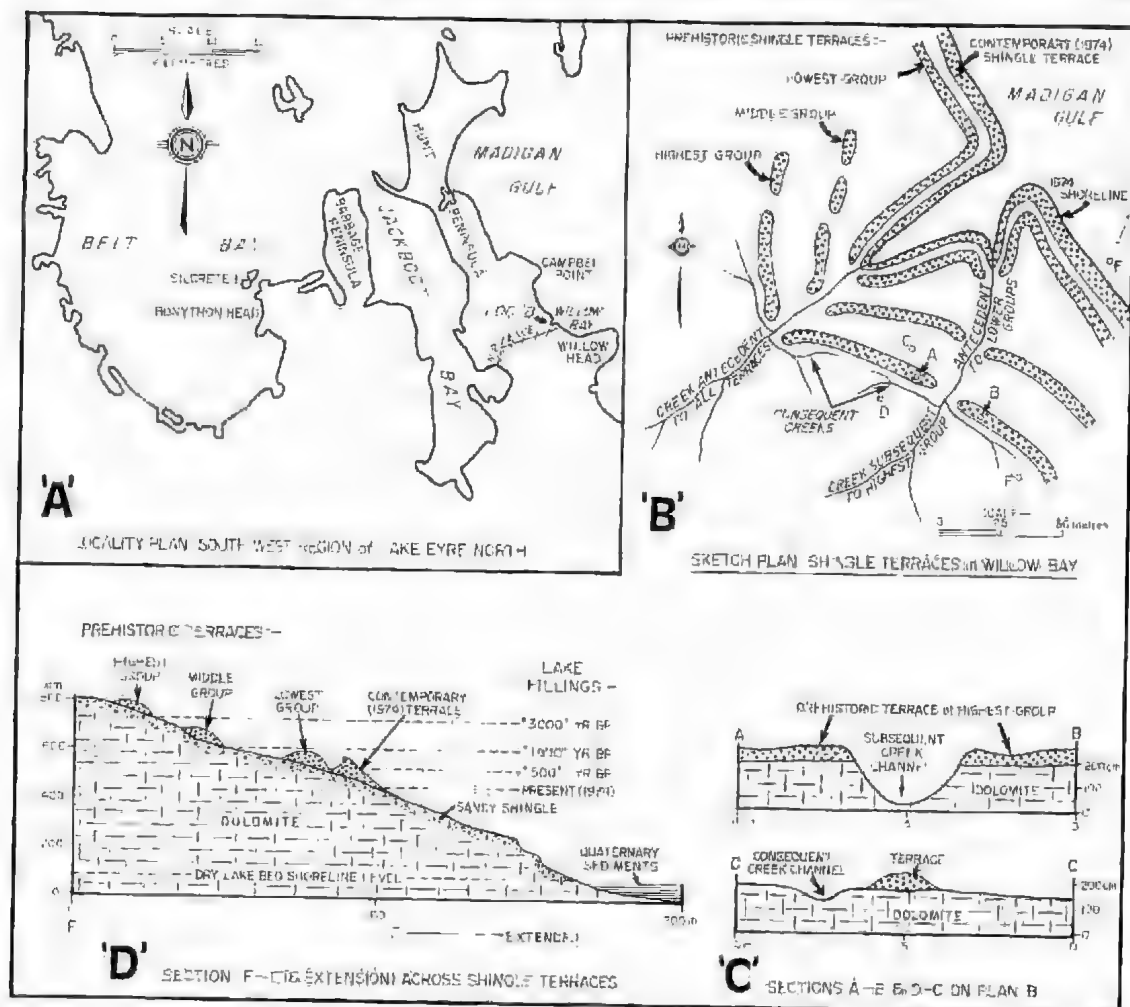


Fig. 1. Wave-built shoreline shingle terraces in Lake Eyre North.

of greater amplitude than in 1974, or terraces with tops more than 90 cm above mean lake level, as the 1974 water depth was more than one half the wave length of average strong wind waves. This was sufficient to allow development of waves as high and long as the limited fetch across the lake could produce. Increases in depth of water, within the limits of beach heights, would not appreciably increase distances of water across the lake as the shores are relatively steep. If average strong winds during prehistoric fillings were similar to those of today, heights and lengths of waves must have been similar to those which built the present day terraces.

Old shoreline shingle terraces

At many places along the shingle-strewn shores, old partly eroded shingle terraces occur

at levels above that of the 1974 terraces, following contours across sloping terrain behind and above the 1974 beaches. Excellent examples occur along the eastern shoreline of Hunt Peninsula between Willow Head and Campbell Point, immediately north of the Elliott Price National Park fence, at numerous places on Babbage Peninsula and Bonython Head in Belt Bay, and on Silcrete Island off Bonython Head (Fig. 1A). Although eroded, the old prehistoric shingle terraces all bear close resemblance in general form and nature to the 1974 terraces, and follow contours conforming to the present shoreline. They were formed in a manner similar to the 1974 terraces, by previous fillings of the lake to depths greater than that of 1974 which was the deepest known filling in white man's history. Wave action which formed the prehis-

toric terraces would seem to have been similar to that of the 1974 filling, as already discussed. Lower rates of evaporation in prehistoric mid to late Recent time could have resulted in greater duration of peak lake-level periods and longer times of terrace formation, than in 1974. However, this would not necessarily have produced terraces higher than the equilibrium height, at a given mean lake level, for a given wave height. From observations, equilibrium terrace height appeared to have been reached after 4 months in 1974. So the terrace top height of 90 cm above mean lake level, attained in 1974, is assumed to have been the equilibrium height attained in the formation of the prehistoric terraces. Whilst longer time of terrace formation is not likely to have produced higher terraces, it could well have built wider terraces in association with wave cut benches. However, after allowing for erosion, the old terraces do not seem to have been wider than the contemporary ones, and there is no general evidence of associated wave cut benches.

Measurements of the relative levels of old shingle terrace tops at many places indicated the occurrence of three groups at successively higher levels above the 1974 terraces and maximum mean lake level. They are described as the lowest, middle and highest groups for the purpose of this paper (Fig. 1B, D). Each is considerably more eroded and obviously older than the one beneath it. They represent three prehistoric fillings of the lake to levels higher than that of 1974. No higher terraces were found on the present shoreline slopes of Hunt and Babbage Peninsulas, or on Silcrete Island. Strand gravels recorded by Williams (1973¹) at distances up to 8 km from the present lake shore, lying outside the field of this investigation, contain *Coxiella* which is absent in the recent shoreline terraces. They may have been disturbed by tectonism, but could represent older, possibly Pleistocene, water levels of an earlier phase of lake history as discussed later.

It was concluded that the highest group of old shingle terraces on the present shoreline slope was built by the deepest filling of Lake Eyre during the Recent geological history of the salina as we know it to-day. Terraces of this group were studied in greatest detail to ascertain as precisely as possible the height and age of the deepest prehistoric filling of the present salina.

Mostly the old shingle terraces of the highest group have been greatly eroded or completely removed. However, in protected places, where less erosion has occurred, their tops reach uniform maximum levels which vary in different areas from 280 cm to 350 cm above the 1974 maximum mean lake level. They reach levels of 350 cm along both eastern and western sides of Hunt Peninsula, 320 cm on both sides of Babbage Peninsula, and 280 cm on Silcrete Island. Comparison with the shape and general nature of the 1974 terraces suggests that the least eroded of the old terraces, which were those selected for measurement, have lost only about 20 cm from their tops. This means that the original maximum level of the old terraces was 370 cm on Hunt Peninsula, 340 cm on Babbage Peninsula and 300 cm on Silcrete Island. It is evident that the highest group of old terraces, in each of the three areas, is of the same age, having been formed during the same prehistoric filling. Therefore, the present differences between the terrace-top levels of the highest group, in the three areas, suggest subsidence, increasing to the west, since the filling which formed the terraces, but investigations over wider areas of the lake must be carried out before any general conclusions can be reached about Recent tectonic movements. The purpose of the present investigation was to gain some knowledge about prehistoric fillings. Therefore, Hunt Peninsula was selected as the most centrally placed area of old shingle terraces, and likely to have been least affected by tectonic movements known to have been prevalent along the western side of Lake Eyre (Williams 1973¹; Wopfner & Twidale 1967).

Prehistoric Fillings

As discussed above, the terrace-top level of the highest group of old shore-line shingle terraces on Hunt Peninsula was 370 cm above the peak mean lake level of the 1974 filling, and the contemporary 1974 shingle terrace-top level was 90 cm above the mean lake level at which the terraces were formed (Fig. 1D). Therefore, the peak mean lake level of the prehistoric filling which built the highest group of old shingle terraces must have been very close to 280 cm above that of the 1974 filling. This means that the peak mean lake level of the highest prehistoric filling of Lake Eyre salina, in Recent time, would have reached a depth of about 640 cm above the lake bed along the southern shores of Madigan Gulf.

about 850 cm in the deepest parts of the gulf, and a level of approximately 280 cm above the 1974 water level in Lake Eyre South and along the Central Australian Railway line.

The levels of the terrace tops in the middle and lowest of the three groups of terraces on Hunt Peninsula measured 230 cm and 140 cm, respectively, above the 1974 peak mean lake level. Allowing for 20 cm of erosion, and 90 cm for the height of the terrace top levels above the mean lake levels at which they were built, the two groups would represent fillings of the lake to depths of 160 cm and 70 cm above the 1974 peak mean lake level (Fig. 1D).

The three groups of old shingle terraces, described above, were built at widely spaced intervals of time, during which many other major fillings must have built terraces, at intermediate and lower levels, which were probably destroyed or modified by redistribution of shingle during subsequent deeper fillings. Any terraces built by a filling to a level intermediate between the depths represented by the lowest and middle groups, during the interval between the building of the middle and highest groups, were partly or wholly destroyed by the filling which built the middle group. Similarly terraces built by fillings to depths less than that of the 1974 filling, including terraces of the 1950 filling, have been modified or removed by the 1974 filling.

Antiquity of fillings

The ages of the three prehistoric fillings of Lake Eyre, to depths greater than that of the 1974 filling, are very difficult to ascertain precisely. The only available evidence is very vague and indefinite, and the only conclusions possible are of the order of magnitude of age rather than exact periods of time.

Extensive searches were made for carbonaceous material within the old shoreline shingle terraces, suitable for carbon dating. No shell material or animal bones were found. No plant material such as driftwood was found, although sticks and fragmentary pieces of wood were plentiful in the contemporary 1974 terraces. Plant roots were found in varying degrees of decay, but it was evident that they belonged to plants which grew on the terraces after they were built. The environment of burial in the old shingle terraces was evidently one of maximum aeration, oxidation and penetration of rain water, leading to complete destruction and loss of all plant material originally included in the terraces.

Shell material was absent from both contemporary and old terraces, suggesting that the latter were built by intermittent fillings between which aridity and dryness of the salina prevented establishment of shell fish. The more remote and higher gravel deposits described by Williams all contain small gastropod shells (Williams 1973¹, and pers. comm. 1973) supporting the suggestion that they were deposited during an earlier pre-salina stage when the lake was permanently filled with water carrying a shell fish community. Studies by King (1956, 1960) suggest that gypsiferous lacustrine clays with *Coxiella* occurring along the southern shores of Lake Eyre are of Pleistocene age, and that younger shoreline deposits and sand ridges originated in association with recent deflation of the lake and development of the present salina.

Fluvial erosion of the old shingle terraces bears evidence of their antiquity. The highest and oldest group has been extensively eroded, and completely removed in many places, whilst the middle and lower groups have each suffered successively less erosion. Rainfall is very low, but this is offset by high runoff from arid surfaces. Fluvial erosion under these conditions could be comparable with that of higher rainfall areas where runoff is reduced by vegetation. Wind erosion is not effective as the shingle is too large to be removed.

Where shingle terraces of the highest group have not been completely removed, they have been breached in places by flowing water during rare occasions of heavy rain. Terraces built across pre-existing or antecedent creeks, trend upstream in U-bends as would contours. Where breached, their eroded ends still turn upstream (Fig. 1B). Terraces built across gently sloping surfaces with no pre-existing creeks, have been breached in places by water held back on the sloping surface, leaving the eroded ends of the terrace "in-line" and not turned upstream (Fig. 1B, C). Such breaches are frequently about 8 m wide, and the newly formed subsequent creek channels running through the breaches have eroded down into underlying weathering dolomite to depths of 150 cm below the bases of the terraces. Tributary consequent creeks carrying water along the top sides of the terraces towards the breaches have eroded channels in dolomite to 50 cm deep (Fig. 1C). Whilst erosion of this kind is very difficult to relate in time, it is evident that the terraces concerned are of considerable antiquity.

The close proximity and relations of the old shingle terraces to the contemporary terraces indicate very little modification of the shoreline in general since their formation, suggesting limited age.

Exudation of highly mineralised ground water, due to aridity, has produced much surface and shallow sub-surface cementation of Pleistocene and early to mid Recent sediments. Gypcrete, silcrete, calcrete and ferruginite have been formed (Williams 1973¹; Wopfner & Twidale 1967), and the processes still appear to be in operation. No cementation has been found in the old shingle terraces or the more sandy and earthy material forming their basal layers, suggesting limited antiquity.

The evidence outlined above is not at all precise or satisfactory in attempting to establish ages in years, but it is all that is, as yet, available. For purposes of geological history, the evidence is more significant, indicating that the old shoreline shingle terraces are almost certainly of mid to late Recent, and most probably late Recent, age. For the purposes of physical geography and hydrology of Lake Eyre, estimates are required for (i) the age in years of the deepest prehistoric filling of the salina under existing environmental conditions, and (ii) the number of years since the lake had been previously filled to the level of the 1974 filling.

After making extensive field studies, taking all factors into account, and balancing the somewhat conflicting significance of different aspects of evidence, it was concluded that the oldest and highest group of shingle terraces could date from more than 1,000 years before present, but less than 5,000 years. Further narrowing of these limits must involve inferred speculation, but in the author's opinion the age may be of the order of 3,000 years, which provides an estimate of the age of the deepest prehistoric filling of the present salina. The middle and lowest groups of old shingle terraces are certainly younger, and could well be of the order of 1,000 and 500 years, respectively. The age of 500 years for the lowest and youngest group of old terraces, occurring just above the contemporary 1974 terraces, provides an estimate of the time since the lake had previously been filled to the level of the 1974 filling.

Acknowledgments

It is wished to acknowledge (i) valuable assistance and co-operation of Muloorina Station which made field investigations possible, (ii) valuable discussion with Mr A. F. Williams of the Geological Survey of South Australia, and (iii) research facilities provided by the Department of Geology and Geophysics, University of Sydney.

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NOTES ON THE RELICT PALM *LIVISTONA MARIAE* F. MUELL. IN CENTRAL AUSTRALIA

BY P. K. LATZ*

Summary

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Comparison of photographs taken after intervals of up to 56 years indicate that the relict palm *Livistona mariae* may reach an age of up to 300 years. Aspects of the ecology of the palm are presented.

Introduction

Palm Valley, situated in the Finke Gorge National Park in the MacDonnell Range system, Northern Territory (Fig. 1) is of considerable interest to tourists and scientists alike largely because of the presence of a stand of the relict cabbage palm *Livistona mariae* F. Muell. This species of *Livistona* is restricted to an area of about 60 km² on the Finke River and its tributaries. It is a relict species separated by about 1000 km from the nearest *Livistona* to the north. The closest relative to *L. mariae* occurs on the Fortescue River in the Hamersley Ranges, W. Aust., a stand in many ways similar to that at Palm Valley. The relict nature of the palms is discussed by Keast (1959), Burbidge (1960) and Chippendale (1963).

Although the explorer Ernest Giles was the first to discover the palms in the Finke Gorge in 1872, he almost certainly bypassed Palm Valley itself, and its discovery is attributed to a Lutheran missionary from Hermannsburg Mission some time later. The valley was investigated by members of the Horn expedition during 1894 (Tate 1896). After a visit to the Valley, Lothian (1959) discussed aspects of the palm's reproductive behaviour.

Chippendale (1959) listed 200 plants found to occur in Palm Valley. Since this time a total of 333 plant species have been recorded from the valley (about a quarter of the total number of species recorded for the whole of central Australia!). About 10 percent of these species can be considered to be of rare or restricted

distribution in central Australia. The majority of these rarer species are restricted to areas in the valley fed by permanent water seepage.

Recently a large gas field has been discovered in the area adjacent to and north of the Park. Two gas bearing wells are situated only a few kilometres north of Palm Valley and tapping of these wells for commercial production is being considered.

The Habitat

The palm has a shallow fibrous root system and is situated in an arid area. Therefore a suitable habitat for its continued survival must have a permanent shallow water supply over an area large enough to support a viable breeding population. The area must also be protected from severe erosion forces or have a stable soil environment, as the palm will not survive scouring of surrounding soil.

Palm Valley appears to be one of the very few areas in the central ranges which meets all of these requirements. The permanent water supply in the valley appears to be associated with the peculiar stratification of this area. The gently sloping conglomerate and sandstone strata percolate water from a large catchment area, down to where the valley dissects these strata. The position of this dissection ensures a continuous permanent seepage area along a considerable distance of the valley floor and lower slopes. Although other springs and seepage areas occur in the Ranges, few, if any, extend over such a continuous area. The Finke River bed below Palm Valley has a permanent

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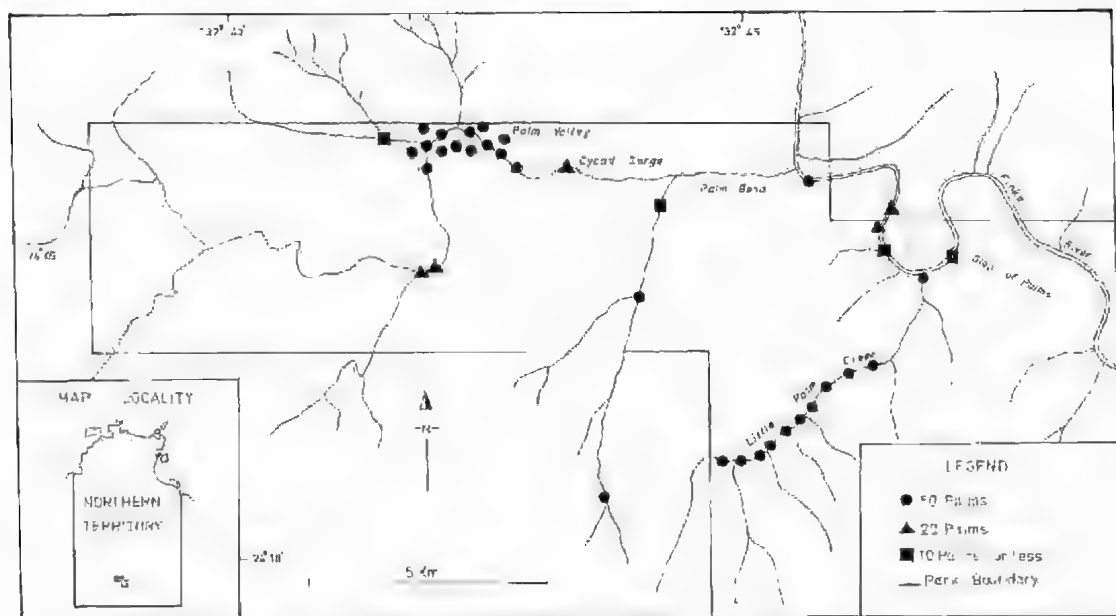


Fig. 1. The distribution and numbers of mature individuals of the cabbage palm *Livistona mariae* in the Finke Gorge National Park, Northern Territory.

shallow water table for much of its length, but it is subject to severe water wash and the few palms found there are restricted to areas which escape the full force of the floodwaters.

Palm Growth Rates and Ages

The author was fortunate in obtaining a number of accurately dated photographs of certain areas of the valley taken as early as 1917. Exact relocation of many of the source points was made possible by the cliff backgrounds of most of the photographs and the fact that the narrow valley is restricted in the number of photographic vantage points.

Of the 13 photograph sites relocated, three are presented in Figs 2–4. The palms in Fig. 2 show the least change of any of the palms investigated and almost all of the individuals present in 1917 (when the photograph was taken) are now still present. The present heights of the living palms were estimated with a Suunto clinometer. By using the cliff background as a scale, palm heights at the time of the earlier photograph were estimated. Distortion due to angle of viewing and to lens aberration was estimated to be less than 10 percent. A mean annual growth rate of 10 cm was estimated for this group of palms.

Palms in Fig. 3, however, have grown approximately 11½ m in 38 years, a mean annual growth rate of 30 cm. Palms in Fig. 4,

which apparently were absent in the earlier photographs, taken in 1918, are now up to 12 m high, a minimum mean annual growth rate of 22 cm.

Palms grown from seed in Miami, Florida, on the bank of a permanent stream, grew to a height of 9 to 18 m in 27 years—an exceptional growth rate of up to 60 cm per year (Lothian 1959). A palm in the cooler climate of Melbourne Botanic Gardens is reputed to have grown to only 3.75 m in 30 years, a growth rate of 12.5 cm per year (Australasian Post, 31 May, 1973).

In its natural habitat, the rate of growth of the palm appears to be mainly dependent on the water supply. The palms showing the fastest growth rate (Fig. 3) are at Palm Bend on the bank of the Finke River about 6 km east of the Valley. This area has a greater depth of fertile alluvial soil and a better water supply than most areas in Palm Valley. Palms in Fig. 4 are situated on one of the best spring areas in the valley, whereas those in Fig. 2 occupy one of the drier areas of the valley, as is reflected by their slower growth rates.

The tallest palms in the valley have reached a height of 25 m. Making allowances for different growth rates at various ages, 100 to 300 years seems a reasonable estimate of the age of the oldest individuals of *Livistona mariae*.



Fig. 2. The upper photograph was taken in 1917 and the lower in 1973.

Effect of Fire

The areas of high palm densities are susceptible to fire as large amounts of plant debris accumulate around the base of the palms. A small area of the valley was subjected to a natural fire in the early part of 1973 and the area was visited by the author approximately 2 months after the event. The fire appeared to have been intense; a palm 28 m high was burnt at the crown and thick ashes (up to 40 cm

deep) were found at the bases of the majority of the palms.

Ninety-six established palms were affected by the fire, thirty of which subsequently died. To ascertain whether certain height classes of the palms had higher survival rates, the heights of all affected palms were measured with a Suunto clinometer. Results indicated that the palms in the height range of 5–8 m had greater mortalities than those in the 1–3 m height



Fig. 3. The upper photograph was taken in 1935 and the lower in 1973. The white bed of the Finke River can be seen in the foreground.

range. However, statistical tests showed no significant difference between the two height populations.

A localised fire was reported in the same area in the 1940's and this fire was severe enough for the smoke to be seen from Hermannsburg Mission, 12 km distant and on the other side of the Ranges. After several subsequent rains, regeneration of palms was reported to be abundant. (A. Latz, pers. comm.) A fire is also known to have occurred

through the stand in Little Palm Creek early in 1959, but little evidence of this fire is now apparent.

It does appear that many of the palms can survive a fire and subsequent regeneration is quite rapid. However, an excessive accumulation of debris over a long time period could provide enough fuel for a more severe and extensive fire than those previously observed, and could effect a higher palm mortality. If this fire followed a few years of poor seed produc-



Fig. 4. The upper photograph was taken in 1918 and the lower in 1973. This area was relocated by using the large rock right of centre in the earlier photograph as a marker. This rock is hidden by palms in the later photograph.

tion, or if a severe flood subsequently removed the majority of seeds, palm densities could be severely reduced.

Palm Numbers

Tate (1896) stated, "... *Livistona mariae* is known by only one colony estimated to comprise not more than a hundred mature individuals". A few were also observed by him along the Finke River as far as Boggy Hole. Keast (1959) estimated a total of at least 300

individuals at all stages of growth were present in the valley.

An exact count of all individuals in the valley is impractical because of the high densities of the palms in some areas and the many younger palms at all stages of growth. However, individuals of reproductive age (ca. 3 m or taller) were found to have at least some of their trunk clear of leaf debris and are relatively easy to count. A count made early in

1973 indicated that about 750 palms of reproductive age occur in Palm Valley.

This is a much greater number than those previously given. Several recent visitors to the valley were asked for their estimates of palm numbers and these ranged from 30 to 800 with an average of 150. These observations tend to show that rough estimations give a lower number than is actually present and may account for the previous low estimates. However, the early photographs, including those not presented in this article, do show lower palm densities than those at the present time.

Stirling (1896) reported that the white basal parts of the inner leaves of the young palms were eaten by aborigines in the area. This would have caused the death of at least some of the palms. This practice has now ceased. In the past, aborigines frequently lit fires to hunt game, stimulate regrowth of some edible plants and signal their presence to other members of the tribe. Only two fires of restricted extent are known to have occurred in Palm Valley during this century. Before this time the aborigines may have burnt the area more frequently to stimulate growth of young palms which could then be used for food.

Contrary to Tate's observations, there are as many palms outside Palm Valley as in the valley itself (Fig. 1). The second largest colony is in Little Palm Creek where 550 mature individuals have been counted. Except for about 6 palms further downstream in the Finkle River, the location of all individuals of *Livistona mariae* known to occur naturally is indicated in Fig. 1. All of the palms of reproductive age have been counted and total 1500. Counts of all of the palms in small representative areas (including established seedlings) show that the palms of reproductive age constitute less than half of the population. Therefore the total number of established individuals of *Livistona mariae* (the total naturally occurring world population) is estimated to be upwards of 3000.

After a good season, each mature palm produces an abundance of seeds with a high natural rate of germination. Although few of these seedlings are able to get their roots into

the rock fissures before they are washed away or die of desiccation, there is present in the populations a wide range of all growth stages. Seeds of other palms are usually slow to germinate and quickly lose their viability unless kept in humid conditions (de Leon 1958), but seeds of the cabbage palm can germinate within months and remain viable for two or more years under dry storage.

Discussion

The cabbage palm is restricted to a small area and its numbers are small. However, it has a relatively fast growth rate, high potential for reproduction, and a relatively rapid ability to recover after fire, all factors that indicate the palm is in no real danger of extinction, provided the present ecosystem is not substantially altered. In fact, numbers appear to have increased somewhat in the last 50 years.

The greatest danger to the continued health of the stand would arise from the lowering of the water table or general disruption or pollution of the seepage area. Fortunately the structure of the sediments probably ensures that this possibility is remote. The relic nature of this unique palm warrants close attention to the general health of the stand and prevention of any disturbances to the area. The planting of palms in other areas of Australia to ensure that replacements are available in case of natural disaster is recommended.

Conclusion

Palm Valley is situated on the edge of a large gas field. The valley is unique botanically, not only because of the presence of the palms, but also because of the high number of other rare plants and the overall diversity of the flora. A reclusive area such as this, is by nature fragile, and therefore any development in this area will require great care and foresight.

Acknowledgments

I acknowledge the help in interpreting and dating the photographs lent to me by my father Arthur Latz. I am indebted to G. Griffin, the ranger at Palm Valley, for his able assistance in gathering facts for this report, and to his employers, the Northern Territory Reserves Board.

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GEOMORPHOLOGICAL EVOLUTION OF PART OF THE EASTERN MOUNT LOFTY RANGES, SOUTH AUSTRALIA

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The scarps associated with the Milendella and Palmer faults are primarily of late Mesozoic-early Tertiary age. It has been claimed that there has been 60-90 m of dislocation on the Milendella Fault since the Miocene, but this is questioned partly because the evidence is equivocal, and partly because in some areas the lower part of the scarp is erosional, being due to the exploitation by streams of intensely weathered rocks in the fault and scarpfoot zones in Quaternary times.

Introduction

The Mount Lofty Ranges have received considerable attention from geomorphologists, but even in studies which are ostensibly concerned with the uplands as a whole it is the western areas that have been investigated in detail (see Benson 1911; Fenner 1930, 1931, 1938; Sprigg 1946). There has been passing reference to particular landforms which occur in the eastern Mount Lofty Ranges (e.g. Fenner 1931, p. 23); there have been reconnaissance studies of small parts of the area (Saies 1968¹; Breuer 1968²; Forrest 1969³; Frahn 1971⁴); and specific features or problems such

as the riverine features of the Finnis valley (de Mooy 1959), the granite forms of the Palmer and Caloote areas (Twidale 1968, p. 95 *et seq.*; 1971, pp. 5-44), and the Permian glacial features of the Strathalbyn area (Maud 1972) have been investigated. Although there has been significant geological mapping of the region (Kleeman & White 1956; White & Thatcher 1957; Mills 1965⁵; Thomson 1969) there has been no consideration of the evolution of the eastern Mount Lofty Ranges as a whole, no attempt to correlate its development with that of the western Murray Basin, and no investigation of the interplay of tectonism and landform development in the area.

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¹ Saies, Janet (1968).—"Geomorphology of the Mannum Falls Area". (Unpubl. B.A. Hons thesis, Univ. Adelaide.)

² Breuer, Margaret (1968).—"The Geomorphology of Harrisons Creek". (Unpubl. B.A. Hons thesis, Univ. Adelaide.)

³ Forrest, G. I. (1969).—"Geomorphological Evolution of the Bremer Valley". (Unpubl. B.A. Hons thesis, Univ. Adelaide.)

⁴ Frahn, D. (1971).—"Geomorphology of the Milendella Area of South Australia". (Unpubl. B.A. Hons thesis, Univ. Adelaide.)

⁵ Mills, K. J. (1965).—"The Structural Petrology of an Area East of Springton, South Australia. (Unpubl. Ph.D. thesis, Univ. Adelaide.)

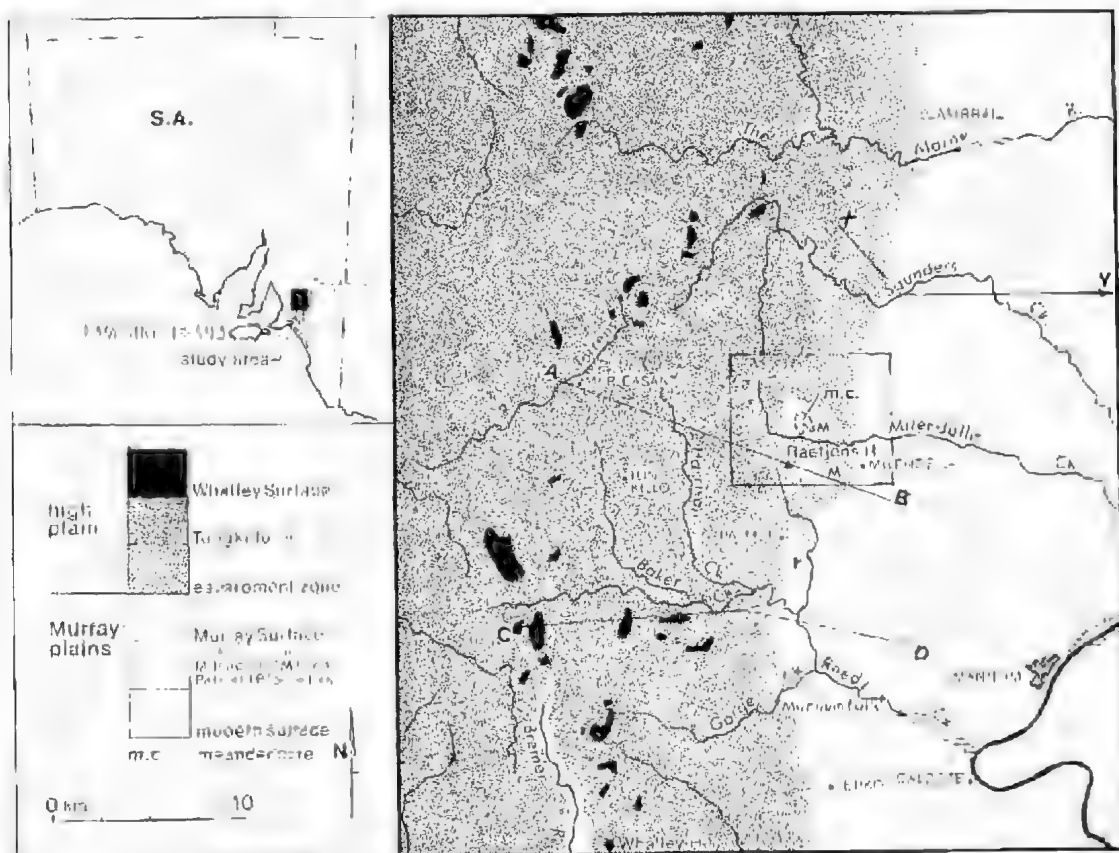


Fig. 1. Physiographic regions of part of the eastern Mount Lofty Ranges, and (inset) location map. The area around Ruetjens Hill and depicted in Fig. 5b is indicated. A-B and C-D are the lines of section shown in Fig. 5a, and X-Y the section represented in Fig. 7.

General Description

The area under consideration lies between the River Marne in the north and Gorge Creek in the south. It falls naturally into three physiographic regions: the high plain, the Murray Plains and the intervening escarpment (Fig. 1).

The Summit High Plain

Standing at elevations of 200–300 m above sea level, the summit high plain or Tungkillio Surface² lies 120–170 m higher than the nearby Murray Plains. It slopes down to the south (from some 430 m elevation near the Marne to 330 m south of Harrisons Creek).

The Surface is eroded in gneiss, schist and granite (Fig. 2) which are essentially unweathered and which give rise to distinctive landform assemblages. Boulders known locally, and inadvisedly (Twidale 1971, pp. 14–17), as 'tors', have developed on the northern part of the Palmer granite outcrop where the rock is well-jointed but not shattered and where split

rocks, perched rocks or loganstones (Fig. 3a) together with the many clusters of boulders form a distinctive landform assemblage. The foliation of the gneisses has been exploited by weathering agents to produce penitent (Ackermann 1962) or tombstone rocks (Fig. 3b), but in other places, as for instance 6–8 km east of Mount Pleasant, the gneiss is more massive and forms low (up to 10 m) angular blocky residuals (Fig. 3c) or miniature castle koppies.

Also standing above the level of the Tungkillio Surface are several scattered low (again up to 10 m) mesas or conical hills which are either underlain by lateritic weathering profiles carrying a ferruginous encrustation, or are capped by alluvial gravels and boulders of predominantly quartzitic composition. These residual hills collectively form what has been called the Whalley Surface³.

The Tungkillio Surface is deeply incised by such intermittent streams as the River Marne, and Saunders, Milendella, Harrisons and

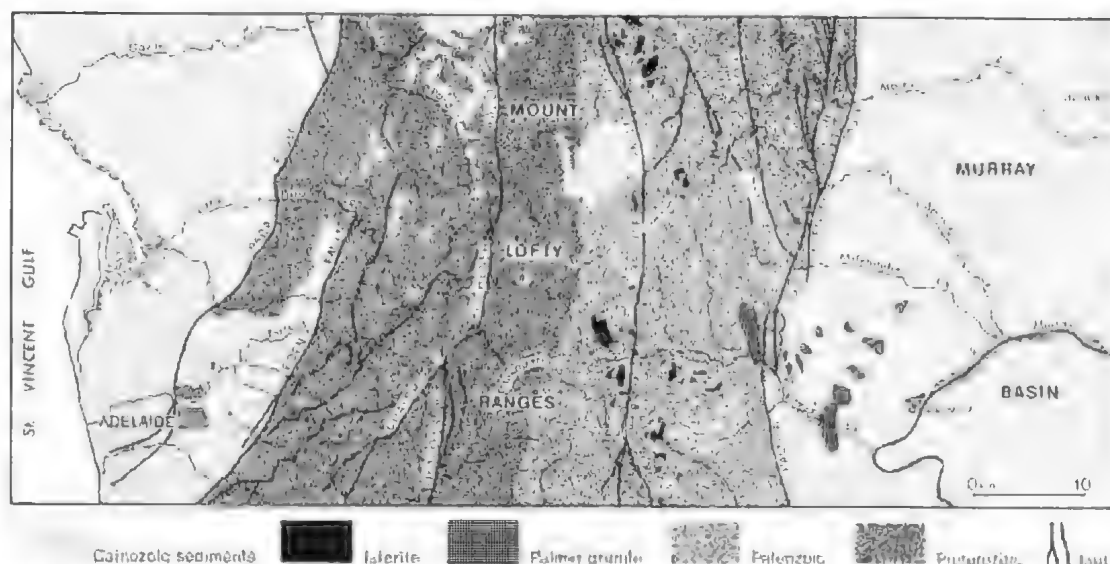


Fig. 2. Generalised geological map of part of the Mount Lofty Ranges (after S. Aust. Geol. Surv. map sheet S1/54-9, Adelaide).

Gorge creeks. Their valleys are however surprisingly narrow in proportion to their depths, and in many places the streams run through gorges or defiles.

The Escarpment

The eastern escarpment of the Mount Lofty Ranges is, like its western counterpart (Fig. 2), a complex feature. However in broad view it comprises two north-south trending scarps which are so gently arcuate that they can be regarded as linear. The two are offset with respect to one another by a distance of some 3 km, the northern component extending as far south as Milendella, the other from the vicinity of Raetjens Hill and south through Palmer (Fig. 2).

The scarps are intensely dissected. The Milendella Scarp is greatly eroded, the zone of dissection being some 4–6 km wide. However, dissection behind the Palmer Scarp extends for only some 2 km. The latter is also lower, being 100–145 m high compared to the Milendella which rises 250 m above the scarp foot.

Various minor breaks of slope of probable structural origin can be discerned on the scarp. In some places the upland scarp displays a basal steepening and scarpfoot depression, as do some of the ridges within the upland (Fig. 4a). In some few sites, prominent flats occur at levels intermediate between the Tungkillo Surface above and the Murray Plains below. One,

the Milendella Bench, is greatly dissected by the present Milendella Creek and its tributaries, but there are nevertheless broad flats at elevations between 260 and 280 m, which are interpreted as remnants of a once continuous flood plain. They stand some 80 m higher than the plains to the east, and descend by way of a steep slope to the Murray Plains (see Tepko 1:50,000 topographic series (6728-III) between grid lines 320 and 347, and 440 and 493; see also Fig. 5a and b). The bluff leading up to the summit surface from the perched bench is precipitous and arcuate in plan. Several features suggest that it is an abandoned meander bluff: its shape, the presence of a central hill interpreted as a meander core within the horseshoe-shaped valley which forms the northerly extension of the bench, and the presence in the valley floor of several metres of alluvium. It was associated with an entrenched meander similar to those found on the present Milendella Creek but of roughly 5–6 times greater radius. The meander loop and core developed when the precursor of Milendella Creek flowed at a level some 80 m higher than at present.

A second bench occurs where Harrison's Creek leaves the uplands to flow across the Murray Plains, where it is known as Reedy Creek (see Tepko 1:50,000 topographic series (6728-III) around MR313374; see Fig. 4b). Less extensive than the Milendella Bench, it stands at an elevation of 150 m above sea

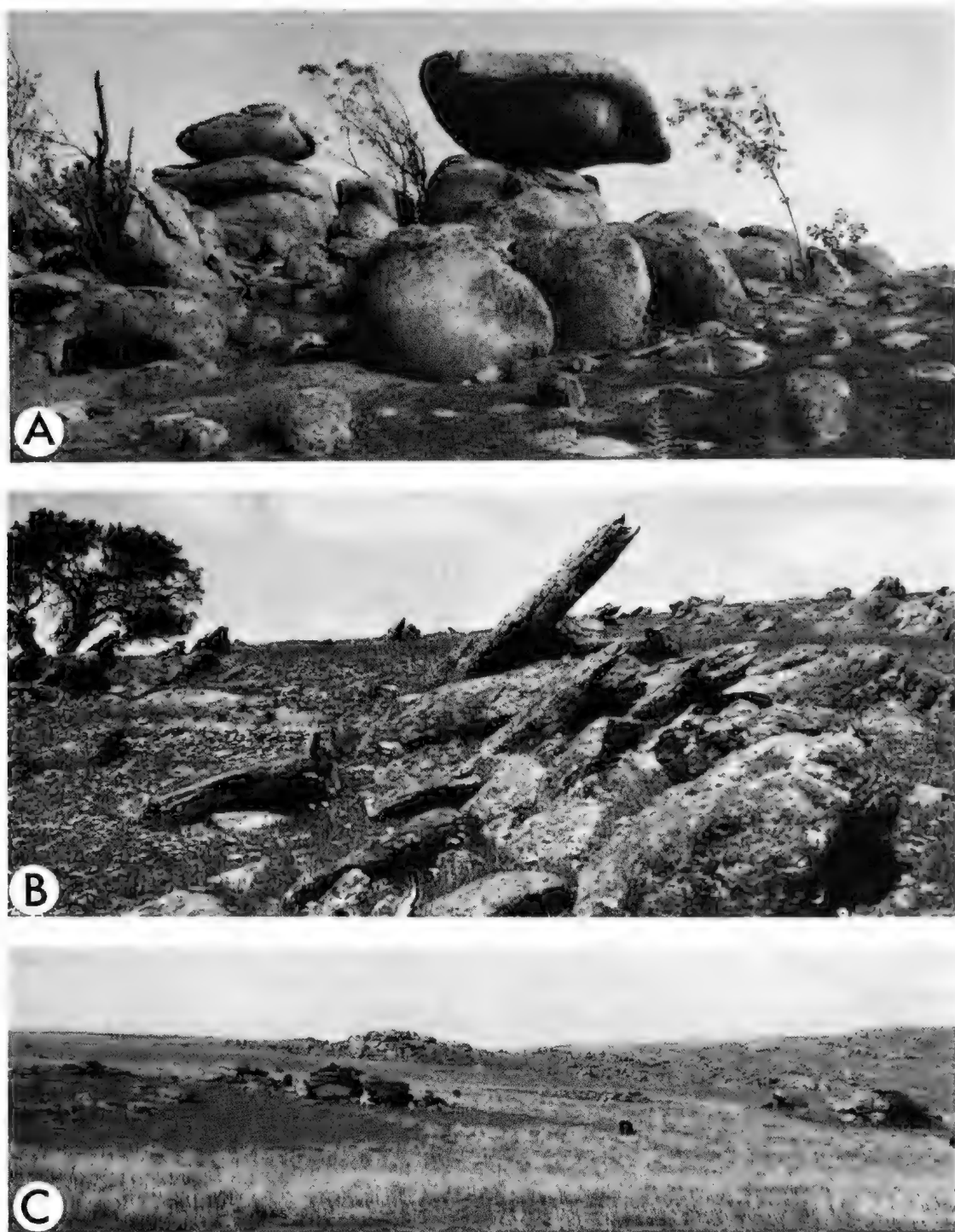


Fig. 3. a. Boulder cluster and loganstone or perched rock on the granite outcrop near Palmer. (C. R. Twidale.)
b. Penitent rocks or monkstones developed on granitic gneiss near Tungkillo. (C. R. Twidale.)
c. Low blocky outcrops of granitic gneiss east of Mount Pleasant. The even skyline is part of the Tungkillo Surface. (C. R. Twidale.)

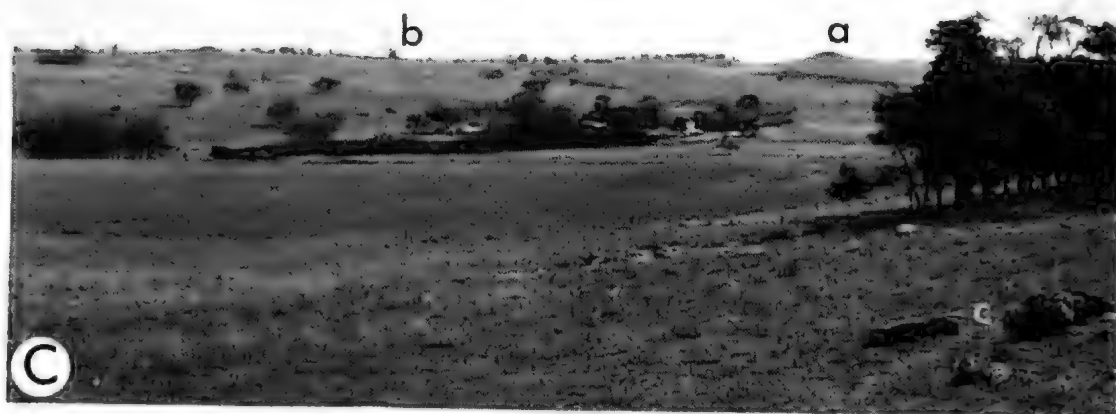
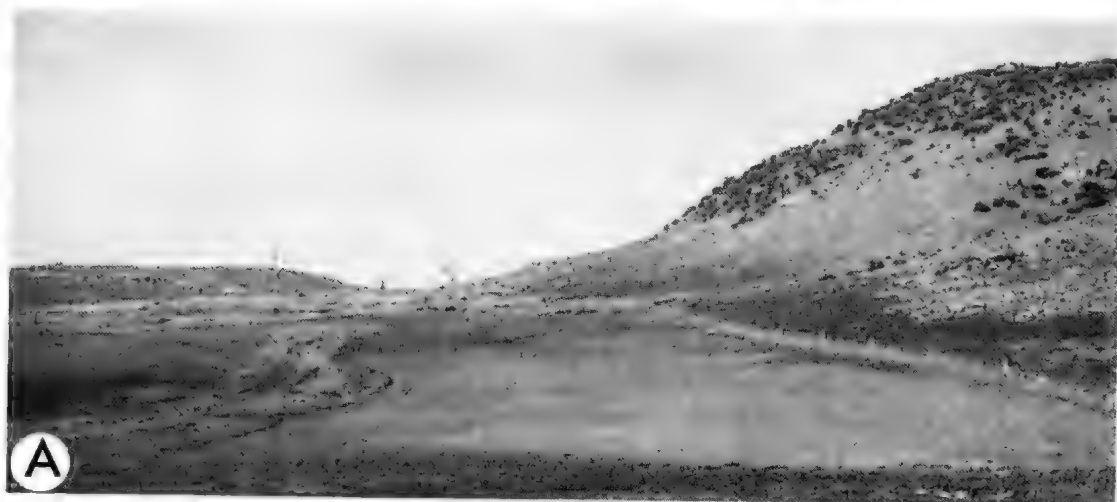


Fig. 4. a. Small scarpfoot depression developed at the base of a gneiss ridge at Raetjens Gap. (C. R. Twidale.)
 b. The Palmer Scarp west of Tepko, showing the Tungkillo Surface, the low scarp (a), the scarpfoot equivalent of the Palmer Bench (b), the break of slope on the hogback scarp (c), the scarpfoot valley (d), and the lower steeper scarp face (e). (C. R. Twidale.)
 c. The Whalley Surface (a) and Tungkillo Surface (b) west of Mount Pleasant. Outcrops of the gneiss country rock are seen in the foreground (c). (C. R. Twidale.)

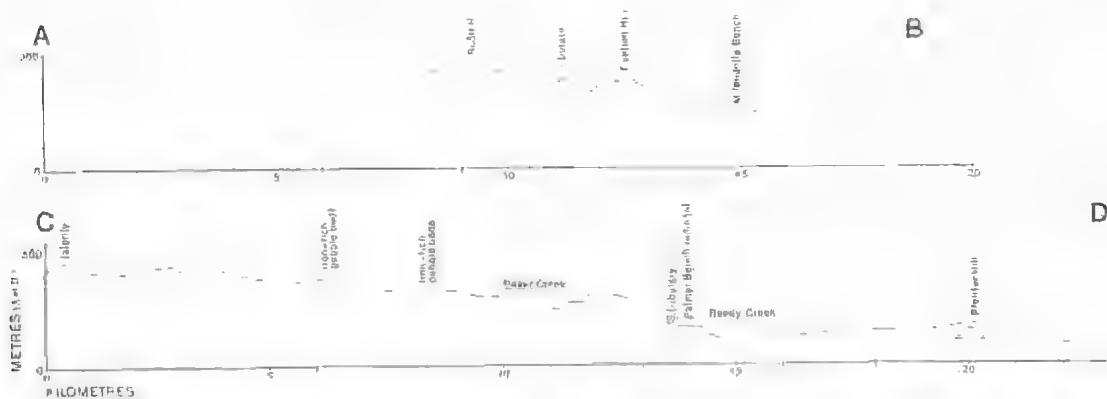


Fig. 5. a. Profiles (A-B and C-D on Fig. 1) across the study area showing the Whalley and Tungkillo surfaces, the east-facing scarps, and the Milendella and Palmer benches. Drawn from S.A. Lands Dept. 1:50,000 topographic sheet 6728-111, Tepko.

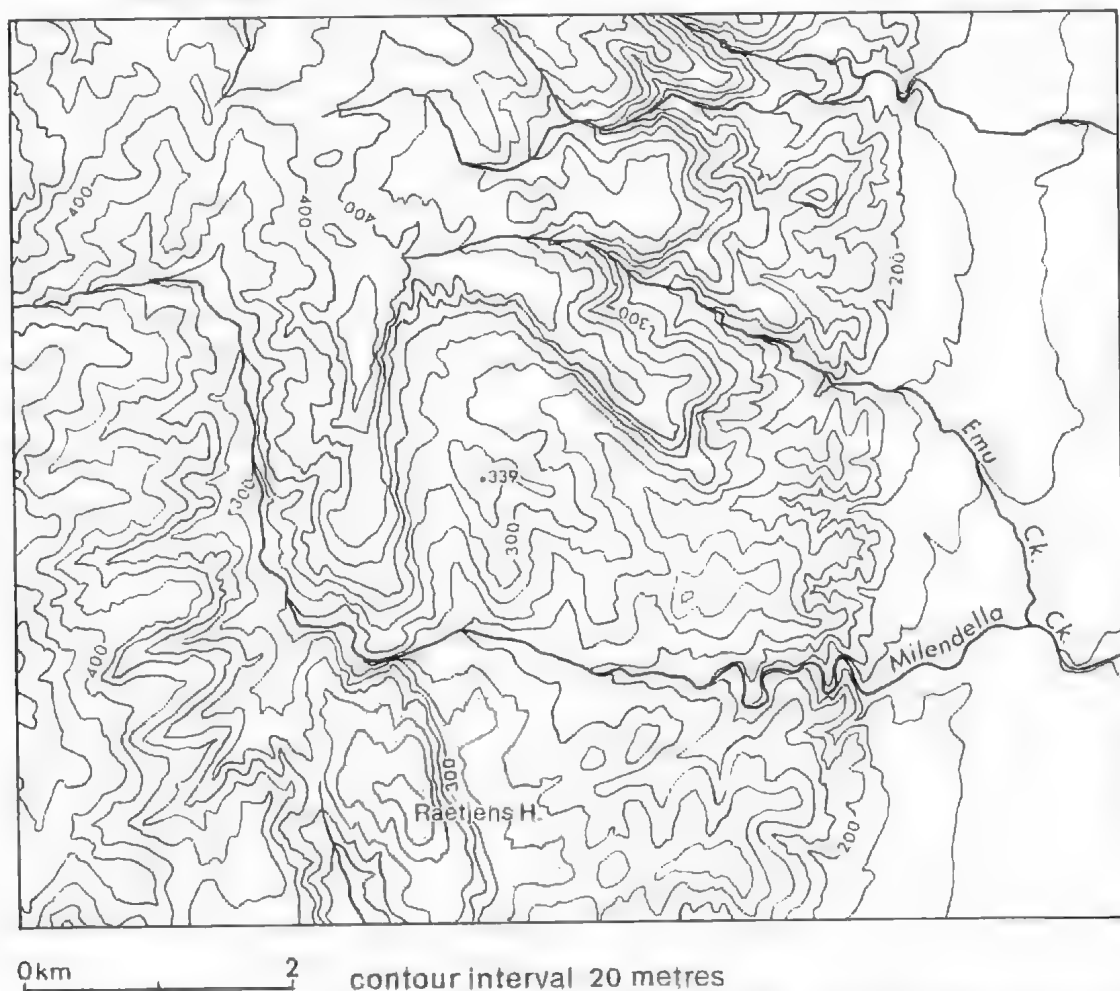


Fig. 5. b. Generalised topographic map of the Milendella Bench showing the old meander loop and the meander core (spot height 339). Drawn from S.A. Lands Dept. 1:50,000 topographic sheet 6728-11, Tepko.

level, 50 m above the adjacent plains and 130 m below the Tungkillio Surface and in detail includes several levels which represent stages in downcutting. This Palmer Bench (so called because the site of the original Palmer township was only a short distance away) carries a mantle of quartzitic blocks, some of which are iron-stained. It has been dissected by Reedy Creek which in this sector displays well-developed entrenched meanders.

Other, similar, perched benches have been noted near the mouth of Pine Valley, south of Tepko, and particularly west of Strathalbyn where there is an extensive dissected bench, but as these are outside the study area they are not considered further.

Murray Plains

The western Murray Plains comprise a rolling lowland which stands 200–150 m high near the scarp foot, to 70–50 m at the cliff top overlooking the River Murray. In several sectors there is a scarpfoot depression up to 50 m deep fronting the Mount Lofty Ranges (Fig. 1).

These western Murray Plains are underlain by Cainozoic strata 80 m or more thick. In the west, Quaternary conglomerates predominate but these thin to the east where Miocene marine strata occur in bays, in tributary valleys, and in the high precipitous bluffs bordering the Murray trench (Fig. 2). Borelog data indicates that the Miocene strata rest on an irregular surface cut in acid and basic crystalline rocks. Basic crystalline rocks are exposed at Black Hill, where the so-called 'norite' has been extensively quarried; similar rocks have been located in bays near Sedan and Walkers Flat. Granitic rocks and schists are exposed extensively in the valley of Reedy Creek, but also in many other minor outcrops.

How did this landscape evolve? Of what age and origin are the plains? What is the nature of the scarp which separates the high from the low plains?

The linearity of these scarps and their association with faults exposed in the gorges of the River Marne and Saunders Creek or inferred from the displacement of strata, suggests that the topographic forms are fault generated and probably fault scarps, i.e. due directly and wholly to tectonic displacement. This is certainly the view of Mills² who with respect to the Milendella Fault, which is of reverse

type, argued that several stages could be detected in its development:

1. Initiation of the fault in the Palaeozoic with the east side upthrown by many hundreds of metres.
2. Early Tertiary erosion and peneplanation with no faulting.
3. Renewal of faulting during the early Tertiary to Miocene with the east side subsiding by about 260 m.
4. Miocene marine incursion with strata overlapping the eroded fault-scarp.
5. Recurrent movement on the fault since the Miocene, the east side being lowered by 60–90 m.

Several aspects of this chronology can be challenged, and in particular the date and extent of faulting are open to question. The problem involves a consideration of the age and character of erosion surfaces identified in the Mount Lofty Ranges and on the adjacent Murray Plains.

Age and Nature of the Summit Surface

The summit surface is a complex feature. The lateritic remnants of the Whalley Surface are crucial to the interpretation of the whole upland. They are sufficiently scattered to suggest that they are relicts of a once-contiguous weathered surface of low relief, over which flowed streams carrying a gravelly and bouldery quartzose bedload. Remnant deposits of these boulder beds occur in places, and a discontinuous mantle of angular quartz fragments forms a veneer on the low divides. The weathering extended only some 10 m beneath the surface but it is notable that the base of significant weathering—the 'weathering front' of Mahbutt (1961)—is everywhere coincident with the local level of the Tungkillio Surface, underlain by intrinsically fresh rock. Thus it is reasonable to suggest that the Tungkillio Surface is an etch plain (Wayland 1934), formed as a result of the stripping of the lateritic deep weathering profile and the consequent exposure of the essentially fresh rock beneath (Figs 4c and 6). The penitent rocks, small castle koppies and boulders typical of various areas of the Tungkillio Surface (Fig. 3) were developed by differential weathering at the weathering front and exposed as a result of the stripping of weathered material.

The age of the Whalley Surface and of the deep weathering is Mesozoic and probably early Mesozoic (Triassic). The laterite remnants can be traced to the southern Mount



Fig. 6. Diagrammatic section through the eastern Mount Lofty Ranges showing the relationship between the lateritised Whalley Surface underlain by weathered bedrock and the etch plain, coincident with the weathering front, of the Tungkillio Surface.

Lofty Ranges where the laterite surface stands high above valleys partially filled by Miocene marine sediments, and where the fault angle depressions resulting from the fault-dislocation of the summit surface contain basal marine sediment of early Tertiary age, and with inclusions of laterite blocks (Glaessner 1953; Glaessner & Wade 1958; Campana 1958). Thus the summit surface and the laterite it carries must be of earliest Tertiary or late Mesozoic age. However, evidence from Kangaroo Island, just across Backstairs Passage from Fleurieu Peninsula, suggests a much older age. There the laterite plateau formed on Cambrian and Permian strata was partially dissected before the extrusion of Middle Jurassic basalts near and just west of the present site of Kingscote. Palaeoclimatic consideration suggest the Triassic as the most likely period for laterite development (Daily, Twidale & Milnes 1974).

Thus by short-distance correlation the Whalley Surface and the associated deep weathering are considered to be of early Mesozoic age. The development of the Tungkillio Surface followed the disruption of the upland, probably by faulting. Streams were rejuvenated and they exploited the contrast in cohesiveness and resistance between the regolith and the fresh rocks beneath, with the result that an etch surface of low relief, the Tungkillio Surface, was initiated. It is still extending.

Disruption of the Summit Surface

In view of the character of the Milendella and Palmer scarps it is obvious that the reason for the disruption of the summit surface could have been a renewal of movement on the two recognised faults. If this were so, rocks similar to those of the nearby upland should be found beneath the Cainozoic strata of the western Murray Basin. Granites and gneisses are exposed widely in the valley of Reedy Creek,

in minor outcrops throughout the western Murray Basin, and they are commonly encountered at shallow depths west of the River Murray. But there is one feature missing, namely buried laterite, though weathered (kaolinised) Cambrian bedrock is recorded in bores beneath the fresh crystallines and the overlying Cainozoic strata. There are also superficial ferruginous encrustations on high plain remnants and at higher elevations than the Miocene strata and therefore of later Cainozoic age, in the Murray Plains, for example just south of the Mannum Falls. Further reference is made to these occurrences below, but no laterite profiles have been found either in outcrop or in bores.

There are a number of possible explanations. For some reason or reasons at present unknown, laterite may not have developed on those rocks of what was to become the down-thrown block; this is rejected as being irrational. Second, the laterite could have been eroded before burial by Miocene and later sediments, but then some remnants should surely have been preserved. Third, the laterite may indeed be preserved beneath the Cainozoic cover, but has not yet been discovered. This is unlikely because many bores have been sunk and though there is some reference to weathered crystallines, there is none to laterite. Fourth, the weathering of the Cambrian rocks could have taken place beneath the Cainozoic cover, but it is unlikely that the oxidation represented by the weathered bedrock could have developed in such conditions. Fifth, the laterite could have been buried and iron oxide duricrust destroyed by groundwater attack in the subsurface. Such dissolution of iron oxide by water charged with organic acids has been shown to be possible (Bloomfield 1957; Coulson, Davis & Lewis 1960; Hingston 1963).

This last explanation seems to be the most likely. All other indications are that the Whalley Surface was dislocated by faulting, with the east side subsiding by a matter of 260 m in the north. The concentration of groundwaters in the scarp-foot zone (see Ruxton 1958; Twidale 1962, 1967) would account for the subsurface elimination of the ferruginous crust.

Thus if it is accepted that faulting occurred after the development of the lateritised summit surface but prior to the Miocene marine transgression, a number of geomorphological changes can be related to this period:

1. The rejuvenated streams began the stripping of the laterite regolith and the development of the Tungillo Surface.
2. The rejuvenated streams incised into the unweathered bedrock creating quite deep, narrow, and in places meandering gorges.
3. As they emerged from the uplands, the streams eroded quite broad embayments in the crystalline basement rocks of the uplands contiguous with the then surface of the Murray Plains. The Milendella Bench stands considerably higher than either the Palmer Bench or bench remnants at the mouths of the Saunders and Marne gorges. This may reflect its development at a stage before faulting had ceased, and its grading to the Miocene shore, or it may indicate local late Cainozoic faulting.

When did faulting begin? There is no direct evidence, but the stratigraphy of the Murray Basin (O'Driscoll 1960; Ludbrook 1969) suggests that part of the region became a restricted marine embayment during the early Cretaceous. The next proven marine transgression took place during the Late Eocene and marine influence continued through to the Middle Miocene. However, though strata of Late Cretaceous age have not been located, they may have been deposited and subsequently been removed by erosion (Ludbrook 1969, p. 159). The fault dislocation was probably gradual and possibly occupied the whole of this late Mesozoic-middle Tertiary period.

Age of the Plains Surface

The broadly rolling plains surface of the western Murray Basin is being dissected by the few through-flowing streams such as the Marne, Milendella and the Harrisons-Reedy systems, which emerge from the Mount Lofty Ranges and persist to reach the Murray. The River Murray trench is a Quaternary feature, though there was an earlier shallow estuary coincident with the present Murray valley as far north as Morgan. In this long narrow and shallow estuary, marine sediments, the Norwest Bend Formation, of Late Pliocene age were deposited (Ludbrook 1958). Remnants can be seen perched high on the modern cliff-tops in many places, occupying a shallow valley cut in the Miocene strata. As the trench now occupied by the river has been incised below these Pliocene strata, it must be younger and there is much general argument as well as specific evidence (von der Borch 1968) to suggest that it is of

Pleistocene age, being related to low glacial stands of the sea.

However, in Pliocene times the regional base level on the western Murray Plains stood 50–70 m higher than it does now, and it is to this higher baselevel that the streams responsible for the erosion of the plains were graded. These streams transported to the then Murray estuary the detritus which in part comprises the Norwest Bend Formation. Thus the Murray Surface is in the study area of Pliocene age. There is some corroboration from the thin ferruginous duricrusts found on some parts of the surface, as for instance just south and south-west of Mannum Falls, for surfaces of comparable age on northern Yorke Peninsula (Horwitz & Daily 1958) and Eyre Peninsula (Twidale, Bourne & Smith 1976) also carry a ferruginous encrustation, as indeed do post-Miocene valley floors in the southern Mount Lofty Ranges (Horwitz, 1960), and the Karoonda Surface of the central Murray Plains (Firman 1973, p. 23).

The occurrence of iron staining, as well as their elevation, suggest that the several perched benches found at the mouths of major upland gorges were also formed at this time, even though they are now separated from the plains by scarpfoot valleys up to 50 m deep. This is corroborated by profiles relating the benches to the main plains surface (Fig. 5a).

Although little is known of the geometric relationship between river discharge, channel width and the radius of entrenched meanders (cf. Bates 1939 and Dury 1954, 1964; with respect to flood plain meanders, also Geyl 1968) the abandoned meander loop preserved on the Milendella Bench suggests rivers of much greater (? occasional) discharge than those active at present.

Thus, during the Pliocene, the scarp foot stood 80 m higher than present at the mouth of Milendella Creek and 50 m above present baselevel where Harrisons Creek debouches on to the plain. Is the post Pliocene scarp tectonic or erosional, or are there elements of both origins present?

The Question of Post Late Cainozoic Faulting

The lower part of the Milendella, and by implication the Palmer, fault scarps are seen by Mills (1965, pp. 436–442) as due to post Miocene faulting. He discovered several outliers of Miocene sediments perched on the scarp north of Milendella, correlated them with Miocene strata found in hures in the Cambrai

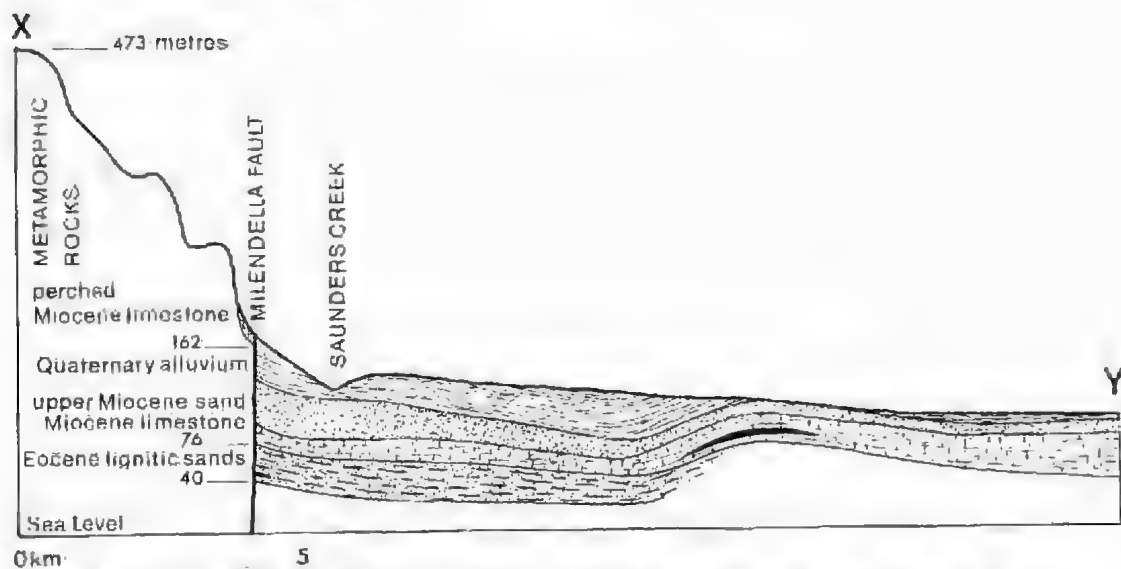


Fig. 7. Section through the Milendella Scarp near Saunders Creek. (After Mills 1965).

and Milendella areas, and took the elevational difference between the two occurrences (i.e. 60 and 90 m) as a measure of post Miocene dislocation on the faults (Fig. 7). He also noted that boulders in the Pleistocene fanglomerates abutting the fault plane display orientation suggestive of recent movement along the plane.

This suggestion of recent and continuing dislocation is borne out by the seismic record (Sutton & White 1968) which shows that the eastern border of the Mount Lofty Ranges is subject to earth tremors. The distinctness of the escarpments both here and to the south suggests geological youthfulness (see e.g. Jenne & Chittleborough 1974). The higher level of the Milendella Bench (see earlier) can also be interpreted as indicating local late Cainozoic dislocation.

On the other hand, the scarps have been deeply and intricately dissected, the Milendella scarp in particular being greatly cut about yet retaining its overall linear morphology. More significantly, the evidence cited by Mills is equivocal and is equally well accounted for in other terms.

The Miocene of the western Murray Basin comprises two major formations: the stratigraphically lower or older Mannum Formation and the higher and younger Morgan Formation (Ludbrook 1969). The two are very difficult to distinguish in the field and can only be differentiated palaeontologically. The faunas of the perched outliers are unfortunately not diagnos-

tic. Mr. J. M. Lindsay reported (pers. comm.) in 1975: "A sample of recrystallised quartzose fine-grained limestone, from a perched outlier of mid-Tertiary rocks 3.5 km north of Sanderton, contained small benthonic foraminifera but no diagnostic forms and no lithological features which would distinguish between Morgan Limestone and Mannum Formation." As the stratigraphic position of the Miocene encountered in bores has also not been determined to this date, it is not possible to identify either the outliers or the strata intersected in bores with certainty and precision. Thus correlation is unwarranted. It can be argued that the topographically higher outliers are Morgan Formation left behind as remnants of circumdenudation after the removal by solution and fluvial action of the bulk of the Formation during the Pliocene and Quaternary, that the Miocene encountered in the bores is Mannum Formation in situ, and thus that no post-Miocene dislocation of any significance is implied by the evidence (Fig. 8). This erosional hypothesis receives support from the character of the Milendella and Palmer scarps. If the scarps were wholly of tectonic origin, then the scarps ought everywhere to be of similar elevation or at least to vary systematically and gradually according to differences in the throw of the fault dislocations. But the scarps in fact vary in height according to their location with respect to scarpfoot streams. Where there are streams either heading back to the scarp foot

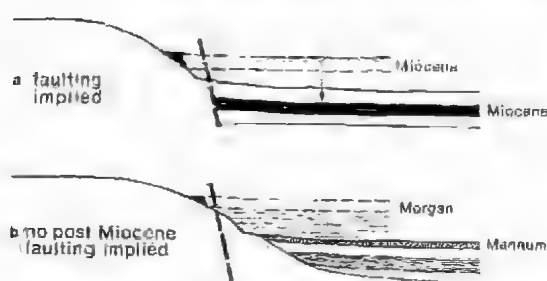


Fig. 8. Two possible modes of evolution for the eastern scarp of the Mount Lofty Ranges.

or debouching from the hills on to the plains, the scarp is higher, there is a faceted scarp with the lower unit steeper than the higher, and there is a distinct scarpfoot valley running parallel to the escarpment (see Figs. 1, 4h and 5a), frequently with intensely weathered rock exposed in the valley floors. In between these sectors are others where there are no scarpfoot streams, where the escarpment is of lesser amplitude and where the hill-plain junction is higher and coincident in elevation with the break of slope on the higher scarps nearby. This suggests that the upper part of the scarp is of fault or tectonic origin, though of considerable antiquity (late Mesozoic or early Tertiary), but that the lower part, where present, is due to erosion by streams eroding the weathered strata of the scarpfoot zone (Twidale 1967); i.e. that the lower scarp is of fault-line type and that no significant recent disloca-

tion is implied. This is not to suggest that there has been no recent movement on the fault: on the contrary, the seismic evidence and the disturbance of pebbles in the conglomerates which abut the fault plane point to recent and continuing dislocation. What is argued here is that the lower, steeper part of the fault scarp is principally erosional and that tectonic dislocation has been a relatively minor factor in its evolution.

There remains the problem of the contrasted state of dissection displayed by the Milendella and Palmer scarps. It is not a matter of contrast in rock type or volume of run-off, for the lithological units of the eastern Ranges run north-south and are essentially similar behind both scarps. It cannot be a question of climatic differences. It may be due to the Milendella and Marne draining a higher scarp, and eroding regressively more quickly to capture the headwaters of the Torrens drainage. More likely however, the dissection of the southern part of the study area has been retarded by the base-level control exerted on the Harrisons-Reedy creek system by the large mass of crystallines exposed west of Caloot. The lower elevation of the Palmer as compared to the Milendella scarp may be a contributory factor.

Conclusion

The development of the eastern Mount Lofty Ranges and the parts of the Murray Plains is summarised below.

| | | |
|-------------------------------|---|---|
| Cambrian | Deposition in Adelaide Geosyncline | |
| Early Palaeozoic | Orogenesis, granite emplacement and metamorphism | |
| Late Palaeozoic | Permian glaciation (not evidenced in study area) | |
| Early Mesozoic | Planation and deep weathering. Marine deposition in lower part of Murray Basin in early Cretaceous (Thornton 1974) | Whalley Surface |
| Late Mesozoic—Middle Tertiary | Faulting, eastern block down. Marine sedimentation Eocene-Miocene. Stream rejuvenation and stripping of regolith | Tungkillo Surface: Scarp formed. Gorges developed |
| Pliocene | Essential withdrawal of sea, only estuarine sedimentation. Planation of Miocene sediments and of embayments in crystalline rocks on face of scarp | Perched benches and Murray Surface |
| Quaternary | Lowering of sea level. Murray Trench formed, tributaries rejuvenated, valleys and scarpfoot zone excavated | Scarp foot valleys, abandonment of scarp benches |

Acknowledgments

The writers wish to thank Dr Brian Daily, Geology Department, University of Adelaide, for a critical reading of the paper, and Dr

Kingsley Mills, Department of Geology and Geophysics, University of Sydney, for helpful discussion and continuing interest in the evolution of the area under investigation.

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THE WOODENDINNA DOLOMITE AND WIRRAPOWIE LIMESTONE – TWO NEW LOWER CAMBRIAN FORMATIONS, FLINDERS RANGES, SOUTH AUSTRALIA

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Summary

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Both formations are widespread in their occurrence, but are best developed in the eastern Flinders Ranges, north of the line of the Blinman, Wirrealpa and Frome Diapirs. The Woodendinna Dolomite and Wirrapowie Limestone record a significant period of supratidal and shallow, sheltered, intertidal deposition respectively within the Cambrian of the Flinders Ranges.

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Introduction

Formations within the Hawker Group (Dalgarno 1964) of the Lower Cambrian of the Adelaide Geosyncline characteristically show frequent changes in both thickness and facies. This results in complex intertonguing of lithological units. The Ten Mile Creek type section (Daily 1956), measured within a syndepositional graben structure northeast of the Orparinna Diapir, represents one of the thickest and most complete sequences of the Hawker Group in the Flinders Ranges. Mapping by the S.A. Department of Mines (Dalgarno & Johnson 1966; Coats *et al.* 1973) and by B. Daily and a number of his students (Gehling¹; Haslett²; Hatcher³; Mount³; Hull³; Daily 1972a) has resulted in the recognition of several significant lithological sequences not present within the Ten Mile Creek type section.

The thick basal Cambrian carbonates in particular exhibit complex and varied facies interrelations and it has become obvious that within the presently established broad divisions, viz.

the Wilkawillina Limestone, the Parara Limestone and the Ajax Limestone (Table 1), several distinctive lithofacies exist. Not only do the present formations contain separate and individually mappable lithologies of significantly different depositional origin but in the past the formation names have in some instances been loosely applied (Dalgarno 1964, pp. 134-135).

TABLE 1
Existing formation names and their sources for the Lower Cambrian carbonate sequences of the Flinders Ranges

| LAKE TORRENS AREA | WESTERN FLINDERS RANGES | CENTRAL AND EASTERN FLINDERS RANGES |
|----------------------------------|-----------------------------|--|
| ANDAMOOKA LIMESTONE (Johns 1968) | AJAX LIMESTONE (Daily 1956) | PARARA LIMESTONE (Daily 1956) WILKAWILLINA LIMESTONE (Daily 1956) |

Whilst it is extremely impractical and undesirable to introduce an excessive amount of formal stratigraphic terminology for the Lower Cambrian carbonate rocks, it is necessary that

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¹ Gehling, J. G. (1971).—The Geology of the Reaphook Hill Area. Honours Thesis, Univ. Adelaide (unpublished).

² Haslett, P. G. (1969).—The Cambrian Geology North of the Wirrealpa Diapir, Flinders Ranges, South Australia. Honours Thesis, Univ. Adelaide (unpublished).

³ Mount, T. J. (1970).—Geology of the Mt Chambers Gorge Region. Honours Thesis, Univ. Adelaide (unpublished).

⁴ Hatcher, M. J. (1970).—The Geology of the Mt Chambers Mine Region, Northern Flinders Ranges. S.A. Honours Thesis, Univ. Adelaide (unpublished).

⁵ Hull, K. G. (1973).—The Lower Cambrian, Puttapa Syncline, Flinders Ranges, S.A. Honours Thesis, Univ. Adelaide (unpublished).

sufficient nomenclature be available to map and describe, on a regional scale, the major rock relationships present within the depositional basin. Careful recognition of mappable units of uniform or repetitive lithological nature should facilitate rather than encumber further work. Such accurate lithological subdivision, coupled with thorough palaeontological evaluation, will result in a more lucid interpretation of the depositional history within the basin. It is with this intention, that the new formation names *Woodendinna Dolomite* and *Wirrapowie Limestone* are proposed.

Present Nomenclature of the Lower Cambrian Carbonate Sequence in the Flinders Ranges

Wilkawillina Limestone

The Wilkawillina Limestone, in its Ten Mile Creek type section, disconformably overlies the Bonney Sandstone Member of the Pound Quartzite, and is extensively dolomitized at the base. In general the unit is massive, pure and pale cream to pink coloured. It consists predominantly of ooid and skeletal grainstones, which may be patchily silicified and recrystallized. An abundant fauna is characteristic of the upper parts, some beds consisting almost entirely of broken skeletal remains of archeocyathids, and associated brachiopods, hyolithids, and trilobites. Algal remains are common throughout and although some cryptalgalaminates and oncolite horizons are present at the very base, stromatolites are virtually absent. Subaerial desiccation features are not represented in the type section. Daily (1956, 1972a) considers the Wilkawillina Limestone to have been deposited on a stable shelf under shallow marine conditions.

Parara Limestone

Flaggy to rubbly dark to black impure limestones with interbedded dark calcareous shales form the Lower Member of the Parara Limestone in the Wilkawillina graben. The Upper Member consists of flaggy and thin bedded dark grey to black aphanitic limestones and thin calcareous shales. Although scantily fossiliferous throughout, the Parara Limestone contains trilobites, hyolithids, brachiopods, sponge spicules, conchostracans and rare archeocyathids (Daily 1956). Stromatolites, flatpebble conglomerates and desiccation features are all completely absent.

Ajax Limestone

Daily (1956) proposed that the term Ajax Limestone should be used for all carbonates

above the Pound Quartzite and beneath the red clastics of the Billy Creek Formation in the Mt Scott Range area. This comparatively thin carbonate sequence incorporates a number of different lithological types. Daily (1972b) has subsequently distinguished a Lower and Upper Member, and in view of the thickness of this unit, any further subdivision of the Ajax Limestone may prove impractical on a regional scale. It is very important to realize, however, that a large number of lithotypes present in the Ajax Limestone are present within the Cambrian carbonate formations mapped elsewhere in the Flinders Ranges (Daily, pers. comm.) and that the change in stratigraphic terminology in the Mt Scott Range area is in large part historical rather than geological.

Proposed New Formations

A significant proportion of the basal Cambrian carbonate sequences, particularly those in the north-east Flinders Ranges, are not readily assignable to any of the above stratigraphic units. Although mapped on the COPLBY 1:250,000 and parts of the PARACHILNA 1:250,000 geological maps as Wilkawillina Limestone, the carbonates show only scant similarity to Wilkawillina Limestone as defined in the type section. In part, these carbonates show greater similarity with the Parara Limestone of the type section, but crucial differences in lithology and depositional environment are apparent on careful examination. It is for these distinctive and widespread basal Cambrian units that the new names *Woodendinna Dolomite* and *Wirrapowie Limestone* are proposed.

Type Section

The type section is located in Wirrapowie Creek and one of its tributaries, about 14 km due east of Point Well Station homestead in the Central Flinders Ranges (Fig. 1). Unfortunately the section presents some difficulties with respect to access, which involves 15 km of travel by four-wheel drive vehicle from a point on the Point Well-Narrina road to Woodendinna Bore, and a further 2 km on foot along a creek to the section. This disadvantage is far outweighed by the completeness of the sequence and the good exposure of both the upper and lower boundaries of both formations.

The combined Woodendinna Dolomite and Wirrapowie Limestone in the type section consist of 392 m of carbonate rocks which overlie, with apparent conformity, *Diplocraterion*

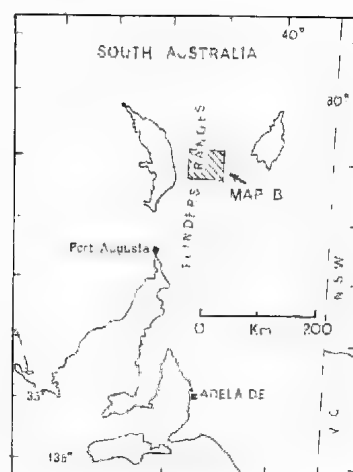
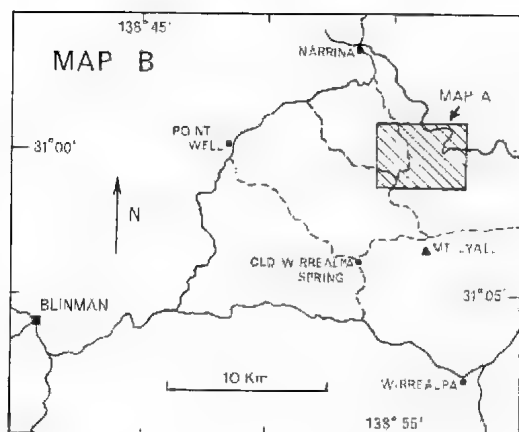
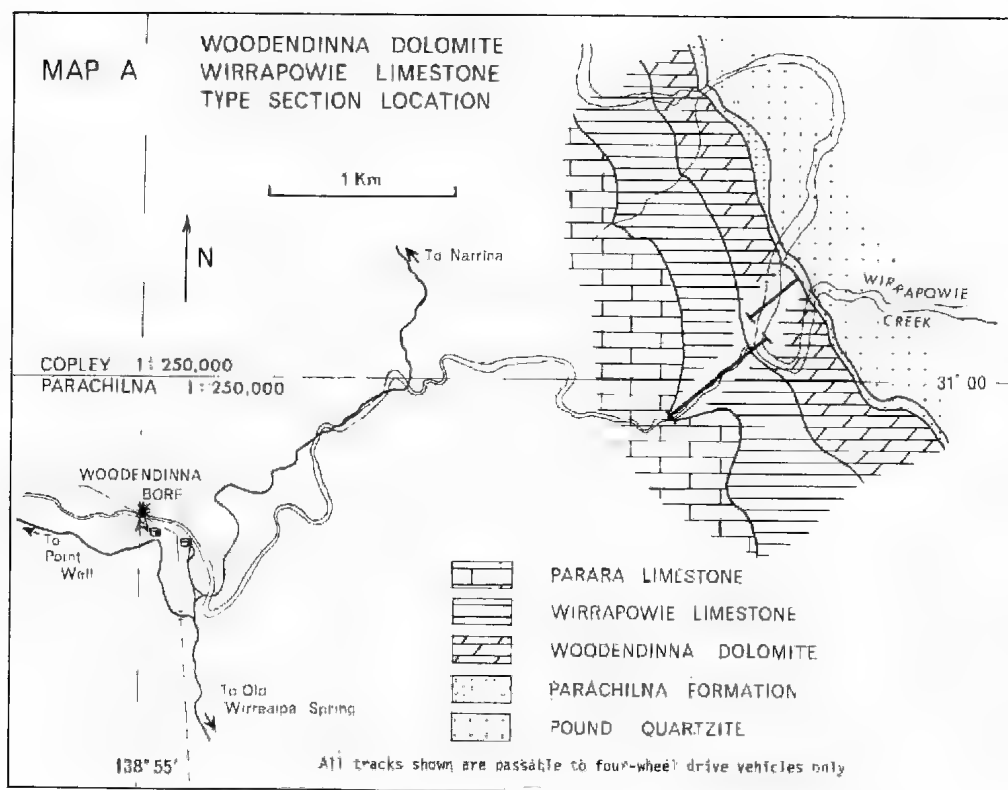


Fig. 1. Location of type section.

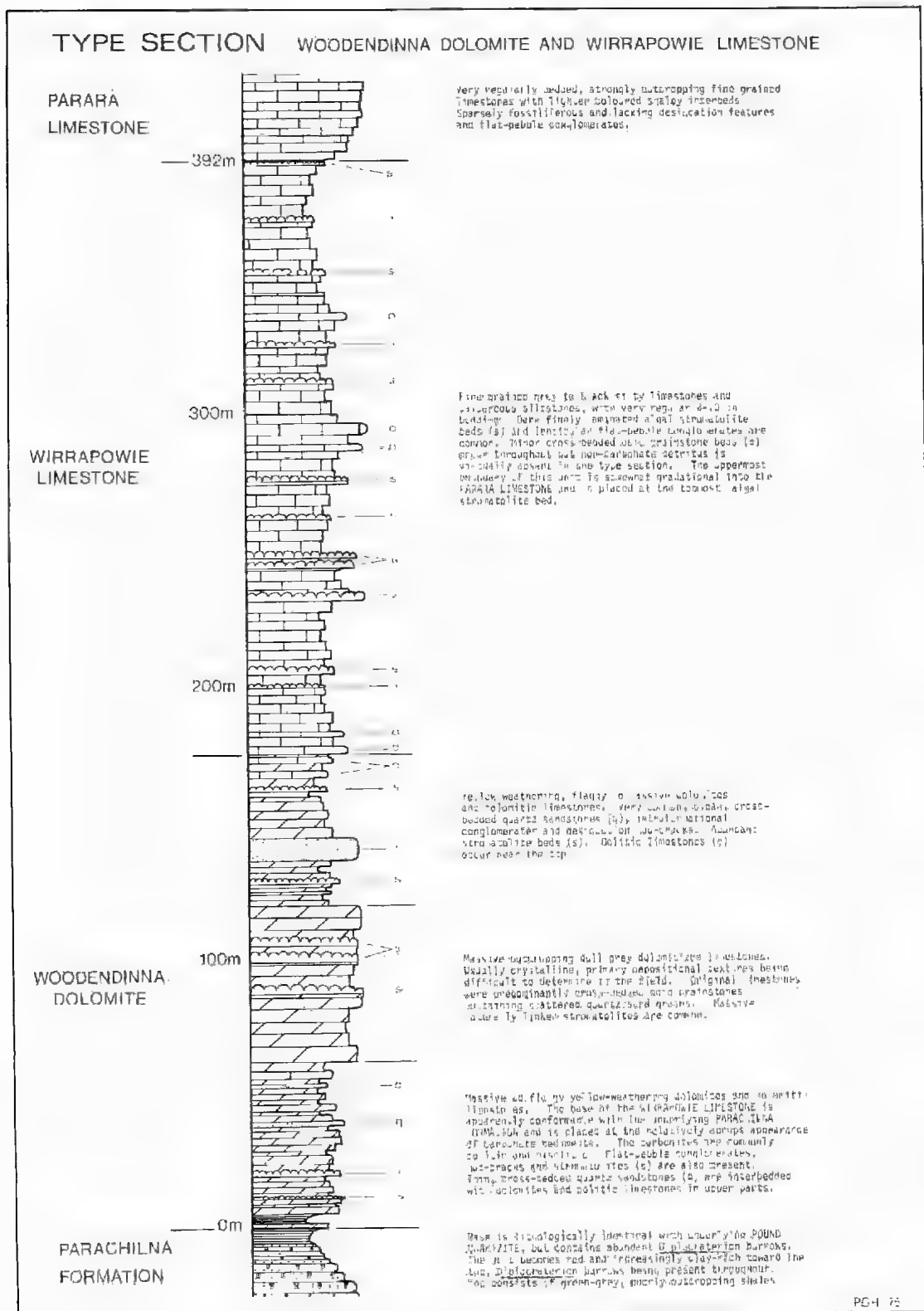


Fig. 2. Type section.

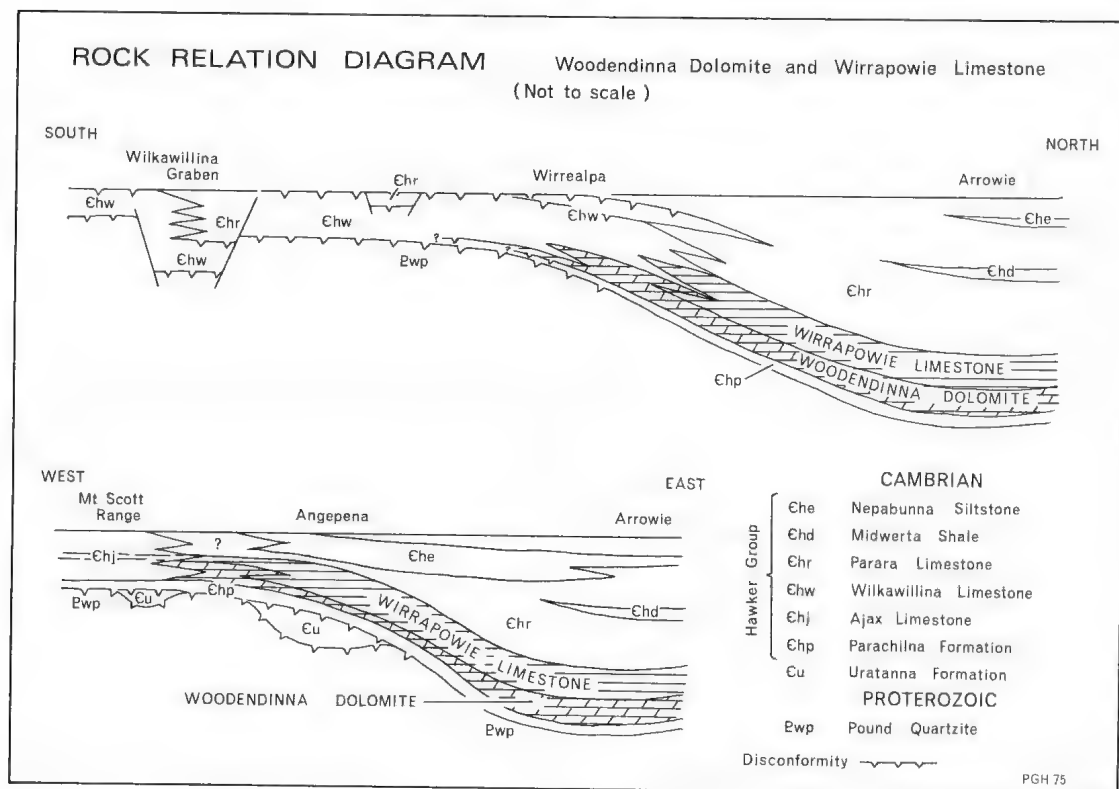


Fig. 3. Rock relation diagram.

sandstones and shales of the thinly developed Parachilna Formation. The entire sequence dips 25° to the SW, on the western limb of a large, slightly southward plunging anticline. In the type section, the Woodendinna Dolomite conformably underlies the characteristically flaggy grey limestones of the Wirrapowie Limestone, the formations being 176 m and 216 m thick respectively (Fig. 2).

Lithological Characteristics

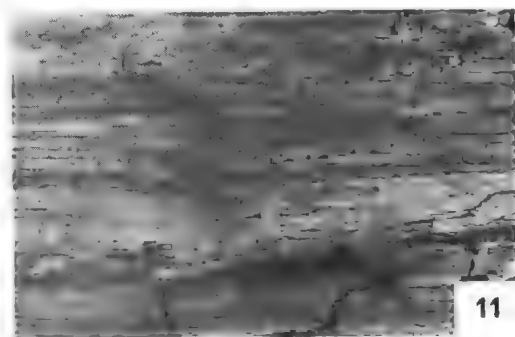
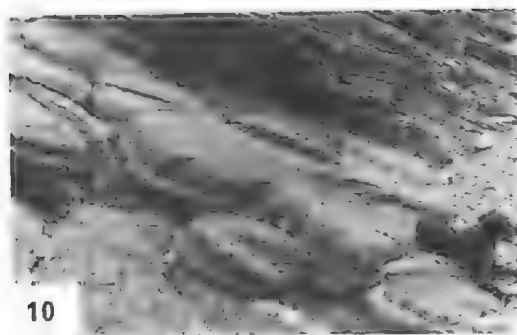
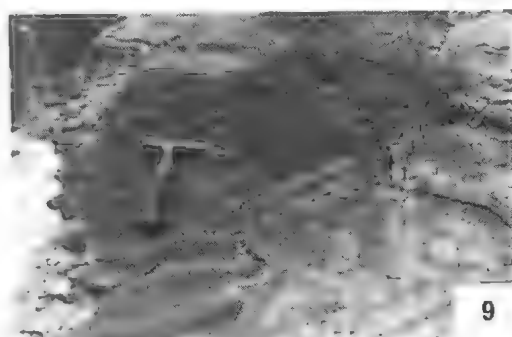
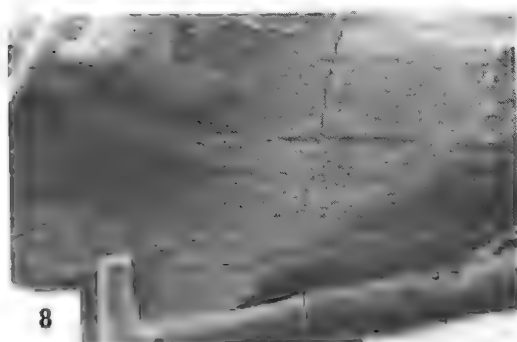
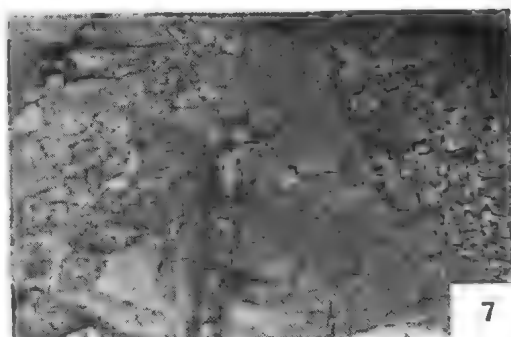
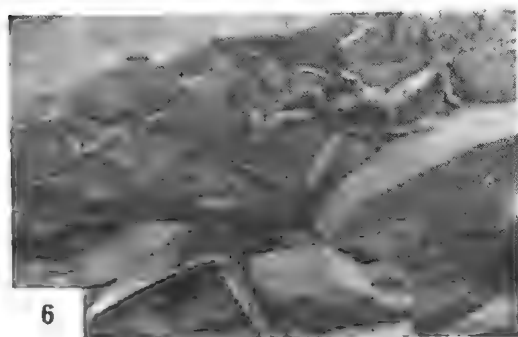
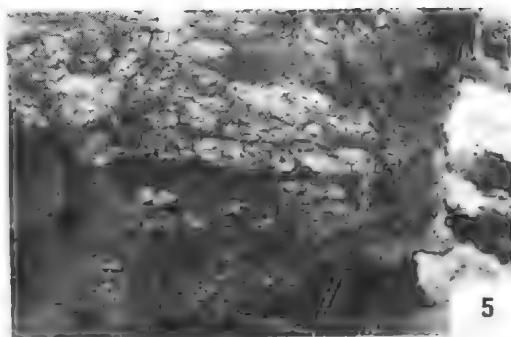
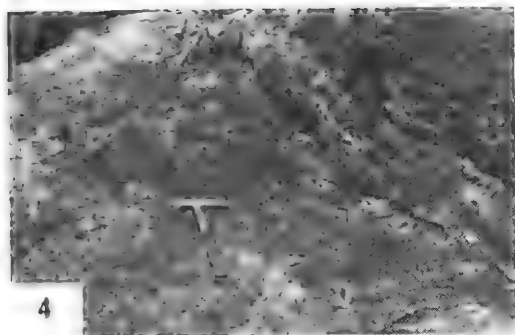
Woodendinna Dolomite

The Woodendinna Dolomite in the type section is apparently conformable upon the Parachilna Formation, and its base is selected at the abrupt appearance of carbonate rocks above the shales and *Diplocraterion* sandstones of the Parachilna Formation. The basal carbonates are partly or completely dolomitized oolitic and pisolitic limestones, interbedded with very minor green shales. Massive to flaggy yellow weathering dolomites with pronounced desiccation features are abundant just above the base, in association with low, broadly domed stromatolites (Fig. 4) and, beginning about 36 m from the base, thin cross-bedded, pure quartz

sandstones. Intraformational conglomerates, often with dolomite clasts in a quartz sandstone or ooid grainstone matrix, are also common (Fig. 5).

Between 69 m and 119 m from the base of the Woodendinna Dolomite in the type section, all carbonates have been extensively dolomitized. This results in the development of a massive dull grey unit which appears, superficially at least, to be lithologically homogeneous, but which has pre-diagenetic lithologies comparable to those directly below and above, but with a greater number of ooid grainstone beds. Some of the grainstones are rich in dispersed quartz sand. Thick, dolomitized algal stromatolite beds and intraformational conglomerates are also common.

Above this dolomitized zone to the top of the Woodendinna Dolomite the sequence consists of interbedded flaggy yellow dolomites, ooid grainstones, stromatolites, flat pebble conglomerates and quartz sandstones, all with beautifully preserved primary sedimentary structures. Desiccation mudcracks, some up to 8 cm deep, are common in the dolomitic mud-



Figs 4-11.

stones (Fig. 6). Ripple marks and chevron-type cross bedding are present in the ooid grainstones and quartz sandstones (Figs 8 and 9). At 135 m from the base, a thick cross-bedded quartz sandstone with abundant creamy yellow dolomitic mudstone clasts is developed. Toward the top of the Woodendinna Dolomite, ooid grainstone beds commonly show a primary rubbly or cobbled upper surface, reminiscent of that found in modern environments on areas of subaerially exposed, partially lithified carbonate sands (Fig. 7).

Wirrapowie Limestone

The base of the Wirrapowie Limestone coincides with the relatively abrupt disappearance of dolomite in the sequence. Flaggy fine-grained, dark grey, limestone and green grey calcareous siltstones dominate the sequence. Desiccation features are less abundant but stromatolites, intraformational conglomerates and minor cross-bedded ooid grainstones are present throughout (Fig. 11). Quartz sandstones are virtually absent. As in the Woodendinna Dolomite, stromatolites are finely laminated, low, laterally linked domes which, on bedding plane exposures, show little if any preferred orientation (Fig. 10).

The Wirrapowie Limestone in the type section is overlain by Parara-type limestones. The topmost limit of the Wirrapowie Limestone is selected at the top of the uppermost algal stromatolite bed. Although a superficial similarity with the Wirrapowie Limestone remains above this limit, the sequence lacks ooid grainstones, flat-pebble conglomerates and evidence of subaerial desiccation. The dark limestones are far more strongly outcropping, purer and more crystalline above the contact. They also tend to be sparsely fossiliferous, with archeocyathids, hyolithids and various brachiopods present. This is in contrast to the underlying Wirrapowie Limestone and Woodendinna Dolomite which are notably depleted in fossils. Apart from algal stromatolites, the only evidence of organic activity found to date are very minor irregular burrows in some dolomitic

mudstones of the Woodendinna Dolomite, and minor trails and apparent bioturbation of bedding which may be found in impure limestones of the Wirrapowie Limestone.

Distribution

The Woodendinna Dolomite and the Wirrapowie Limestone form the basal Cambrian carbonate succession over much of the Flinders Ranges. They are best developed in the eastern part of the ranges, north of the line of outcrop of the Blinman, Wirrealpa and Chambers diapirs (see Fig. 3). In this region their combined thickness ranges from 300 m to 500 m and they appear to thin gradually to the west, where comparable lithologies are thinly developed in the Ajax Limestone at Mt Scott (Daily, pers. comm.) and the Andamooka Limestone in the vicinity of Yarrowurtia Cliff (Wopfner 1969; Daily 1972a). To the south, along the above-mentioned line of diapirs, the Wirrapowie Limestone thins very abruptly and is overlain by, and interfingers with, Wilkawillina Limestone. Syn- and post-depositional tectonism along this line of diapirs, and the consequent development of complex local facies variations, has complicated the regional facies relationships along this line. Lateral interfingering of the Wilkawillina Limestone and the Wirrapowie Limestone is strikingly demonstrated, however, in outcrops just north of the Wirrealpa Diapir (Haslett, in press). Abrupt lateral change southward from Wirrapowie Limestone may also be seen in the vicinity of Eregunda Creek. In addition, Hatcher⁶ indicates a similar southward thinning of a wedge of Wirrapowie-type limestones within the northern part of an area of thickly developed Wilkawillina Limestone near Mt Frome.

In the north-eastern Flinders Ranges, the Wirrapowie Limestone is in all cases overlain by Parara-type limestones. To the best of the author's knowledge, Wilkawillina Limestone is absent from the north-eastern Flinders. Those rocks which are mapped as Wilkawillina Limestone in this area on the COPLEY 1:250,000 Geological Map are assignable to the Wood-

- Fig. 4. Bedding plane exposure of stromatolites, Woodendinna Dolomite.
 Fig. 5. Dolomite clasts in intraformational conglomerate, Woodendinna Dolomite.
 Fig. 6. Well developed mudcracks on the underside of a bedding plane, Woodendinna Dolomite.
 Fig. 7. Cobbled upper bedding plane surface of ooid grainstone, Woodendinna Dolomite.
 Fig. 8. Chevron-type cross beds in quartz sandstones, Woodendinna Dolomite.
 Fig. 9. Ripple marks on bedding surface of a thin quartz sandstone, Woodendinna Dolomite.
 Fig. 10. Squat stromatolite bioherms on bedding plane, Wirrapowie Limestone.
 Fig. 11. Impure flaggy-bedded limestones of the Wirrapowie Limestone. Note the lenticular aggregates of intra-formational conglomerate.

Woodendinna Dolomite and Wirrapowie Limestone in the lower part and obviously hitherto undifferentiated, and in the upper part can be much more justifiably related to Parara Limestone lithologies than those of the Wilkawillina Limestone.

Thin but well developed Woodendinna Dolomite does occur south of the line of the Blinman-Wirralpa-Chambers diapirs along the southern limb of the westward plunging anticline near Mt Lyall (see PARACHILNA 1:250,000 Geological Map). Here it is overlain with apparent conformity by the Wilkawillina Limestone. Further south, toward the Wilkawillina Gorge area, in the Central Flinders Ranges, the Woodendinna Dolomite rapidly thins in response to erosion, or nondeposition or both. At the Ten Mile Creek type section itself, Wilkawillina Limestone disconformably overlies the Bonney Sandstone Member of the Pound Quartzite (Dalgarno 1964; Pierce⁶).

The very highly dolomitized basal Wilkawillina Limestone in this section, however, superficially resembles parts of the Woodendinna Dolomite, but due to the degree of diagenesis, the original nature of these basal carbonates has not been resolved. For convenience they are considered at this stage to represent dolomitized Wilkawillina Limestone lithofacies.

In the east-central Flinders Ranges, Gehling¹ describes approximately 25 m of carbonates, which are lithologically similar to those of the Woodendinna Dolomite, from the base of the Cambrian carbonate sequence at Reaphook Hill.

Along the entire western outcrops of the Cambrian sequence, from Parachilna Gorge south, a thin sequence of flaggy grey limestones, dolomitic mudstones, stromatolites, flat pebble conglomerates, and interbedded sandstones, occur beneath typically fossiliferous Wilkawillina Limestones. These beds are assignable to the Woodendinna Dolomite and the Wirrapowie Limestone and roughly correspond to what Dalgarno called the Lower Member of the Wilkawillina Limestone (Dalgarno 1964), although as stated above, these lithologies are not present within the defined type Wilkawillina Limestone. Dalgarno & Johnson (1963) report significant thicknesses of Wirrapowie-type limestones from just north

of Brachina Creek to south of Mt Aleck, and Dalgarno (1964) records similar rock types in the vicinity of the Chase Range. More recent work has confirmed the presence of both Woodendinna- and Wirrapowie-type carbonate sequences in these southern and south-western parts of the Flinders Ranges (Daily, pers. comm.).

Depositional Environment

From the above descriptions, it is apparent that although the Woodendinna Dolomite and Wirrapowie Limestone are distinctively different in gross mineralogy and in field appearance, they share a number of lithological similarities. They are intimately associated with one another both temporally and spatially and clearly have formed in closely related depositional environments.

The Woodendinna Dolomite shows numerous features characteristic of deposition on emergent high intertidal and supratidal mudflats. Prevalent desiccation mudcracks record repeated periods of subaerial exposure, and the highly restricted nature of the environment is suggested by the paucity of fauna and dominance of primary dolomitic mudstones or pene-contemporaneously dolomitized carbonate mudstones. The only organisms capable of tolerating the extremes of restriction and desiccation of the environment were algae, as evidenced by the abundance of stromatolites in the sequence.

Cross-bedded ooid grainstones and quartz sandstones record brief episodes of high energy conditions penetrating the mudflats. These conditions, which probably occurred during periods of storm activity or times of unusually high tides, resulted in the spreading of sheets of coarser clastics from more open marine areas, over the exposed mudflats. Quartz sandstones in the Woodendinna Dolomite show considerable variation in their lateral development, reflecting the local availability of a quartz sand source, which in many cases probably corresponded to areas of exposed, un lithified Pound Quartzite.

The Wirrapowie Limestone has developed in a sheltered but less restricted upper intertidal to lagoonal environment. The absence of dolomite and the rarity of desiccation mudcracks suggest that only limited exposure and restriction prevailed. The sequence lacks coarse detri-

⁶ Pierce, P. R. (1969).—The Cambrian geology south of the Wirralpa Diapir, Flinders Ranges, South Australia. Honours Thesis, Univ. Adelaide (unpublished).

tus, current bedding and any preferred elongation of stromatolite bioherms indicating that energy conditions were in general still very low. As described above for the Woodendinna Dolomite, however, thin grainstone sheets attest to the periodic penetration, probably during storms, of high energy conditions into the sheltered tidal mudflat environment.

Acknowledgments

The writer wishes to acknowledge the use of the facilities of the Geology Department, University of Adelaide, and to thank both Dr Daily for his generous assistance over a considerable period of time, and Mr C. R. Dalgarno who read a draft of this paper and offered valuable criticisms.

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THE SOUTHERN AUSTRALIAN SPECIES OF SPYRIDIA (CERAMIACEAE: RHODOPHYTA)

BY H. B. S. WOMERSLEY* & SALLY A. CARTLEDGE*

Summary

WOMERSLEY, H. B. S., & CARTLEDGE, Sally A. (1975).- The southern Australian species of Spyridia (Ceramiaceae: Rhodophyta), Trans. R. SOC. S. Aust. **99**(4), 221-233, 30 November, 1975. Four species of Spyridia are recognised on southern Australian coasts. *S. filamentosa* (Wulfen) Harvey (including *S. biannulata* J. Agardh, *S. breviararticulata* J. Agardh, and *S. spinella* Sonder) is common in sheltered to moderately rough water, *S. dasyoides* Sonder (including *S. opposita* Harvey and *S. prolifera* Harvey) is fairly common on rough-water reefs and in deeper water. *S. squalida* J. Agardh (including *S. wilsonis* J. Agardh) is a less common, usually deep-water, species. *S. tasmanica* (Kuetzing) J. Agardh occurs in relatively calm localities but where there is often a strong current. The Australian species differ in vegetative aspects such as arrangement and diameter of the ramelli, but agree well in the development of the thallus and reproductive structures, and emphasize the generic uniformity of the species ascribed to Spyridia.

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Summary

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Four species of *Spyridia* are recognised on southern Australian coasts. *S. filamentosa* (Wulfen) Harvey (including *S. biannulata* J. Agardh, *S. breviaristulata* J. Agardh, and *S. spinella* Sonder) is common in sheltered to moderately rough water. *S. dasyoides* Sonder (including *S. opposita* Harvey and *S. prolifera* Harvey) is fairly common on rough-water reefs and in deeper water. *S. squalida* J. Agardh (including *S. wilsonis* J. Agardh) is a less common, usually deep-water, species. *S. tasmanica* (Kuetzing) J. Agardh occurs in relatively calm localities but where there is often a strong current. The Australian species differ in vegetative aspects such as arrangement and diameter of the ramelli, but agree well in the development of the thallus and reproductive structures, and emphasize the generic uniformity of the species ascribed to *Spyridia*.

Introduction

While *Spyridia* is a distinctive and easily recognised genus of the Ceramiales, the taxonomy of the southern Australian species has been confused. Some 10 species have been credited to the region, but the only recent account of the species by Lucas & Perrin (1947) and a key by May (1965) offer little help in recognising or separating the species.

The type species of *Spyridia*, *S. filamentosa* (Wulfen) Harvey, has recently been described in detail by Hommersand (1963, p. 177), who reviewed earlier studies and clarified its vegetative and reproductive features. Indian material of this species has been studied by Krishnamurthy (1968). Other species referred to *Spyridia* agree well with the type in general morphology, presence of nodal and internodal cell bands, branches of limited growth (ramelli or "brachyblasts") and unlimited growth, and in reproductive features. However, the features which Hommersand (1963, p. 177) used to distinguish *S. filamentosa* from other species of *Spyridia* do not apply satisfactorily to the Australian species. Cortication by tiers of nodal

and internodal cells is found in all species (the cell shape varies considerably in *S. filamentosa*), and all species have radially disposed ramelli (opposite in *S. dasyoides*) which (except *S. squalida*) commonly have mucronate end cells.

Growth of the uniaxial thallus is from an apical cell which cuts off a row of short axial cells which develop into a branch of unlimited growth, from each cell of which one or more ramelli develop laterally. The ramelli are of limited growth, developing rapidly to between 10 and 30 cells long by divisions of their apical cell, and following cessation of cell division they expand by cell elongation to their mature length of generally 1-3 mm. The axial cells also cut off in alternating sequence a ring of periaxial† cells, which form a band around the node between two axial cells. Each of these periaxial (nodal) cells cuts off two cells from its lower end, and these elongate and become attached by pit-connections to the nodal cells of the next lower segment. Thus the thallus shows bands of shorter and broader nodal cells alternating with the bands of internodal cells,

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† This term is used for cells cut off from, but of different form to, an axial cell. Cells of similar form to the axial cell, as found in the polysiphonous families of the Ceramiales, are still referred to as pericentral cells.

which are longer, narrower, and approximately twice as many as the nodal cells. Further cortication occurs some distance from the branch apices, from descending rhizoidal cells developed from the nodal cells, and this obscures the regular pattern of nodal and internodal cell bands, especially in certain species (e.g. *S. squallida*).

The cells of the ramelli each cut off a ring of 6-8 cells from their upper end, and these develop into a nodal band 1-3 cells broad in *S. filamentosa*. *Spyridia* is readily recognised by the alternating nodal and internodal bands, and ramelli with corticated nodes.

Reproductively *Spyridia* is also distinctive, especially in that the carposporophyte becomes surrounded by pericarpic filaments developed from the segments above and below the one bearing the procarp. These filaments can give the appearance of a cystocarp with a well developed pericarp wall, being held together by a mucilaginous sheath and some lateral pit-connections, but they disintegrate fairly readily in preserved material.

Procarpis (3-6) are produced on small lateral branchlets of restricted growth. According to Hommersand (1963, p. 191), three pericentral (periaxial) cells are normally formed in each fertile segment, one of which (the supporting cell) bears the carpogonial branch, and each pericentral forms an auxiliary cell. Hommersand reported that the carpogonium fuses with the third cell of the carpogonial branch which then connects with the auxiliary cells by means of connecting cells. Thus two (or rarely three) gonimoblasts are initiated and the mature cystocarp is commonly bilobed. Krishnamurthy (1968, p. 48), however, observed only two pericentral cells per fertile segment in material from South India, and considered that the fertilised carpogonium divided into two cells, each of which fused with an auxiliary cell.

Spermatangia cover several cells in the lower part of the ramelli, usually excluding the basal cell. They are derived from filaments originating from the nodal cells, which grow over the two adjacent cells, then cut off spermatangial mother cells before forming the continuous surface layer of spermatangia.

Tetrasporangia occur on the lower cells of the ramelli, being sessile and mostly on the upper (adaxial) side. Hommersand (1968, p. 196) considers that they arise directly as protrusions from the axial cell, while Krishnamurthy (1968, p. 47) considers that they are formed from periaxial cells.

Some 10 species of *Spyridia* have been recorded from southern Australia. This study recognises only four species, including *S. filamentosa*. The thallus development and morphology, and the structure of reproductive organs, are very similar to those of *S. filamentosa*, and the Australian species differ mainly in vegetative features. The descriptions below are therefore confined largely to recognition of the species, with brief notes only on reproductive details.

Key to southern Australian species

1. Ramelli robust, opposite and decussate, usually 100-150 μ m thick with isodiametric cells and nodal bands 3-5 cells broad *S. dasyoides* (p. 231)
1. Ramelli slender, single or whorled but not opposite, less than 70 μ m thick, usually with cells longer than broad, and nodal bands 1-3 cells broad 2
2. Ultimate branchlets stout (1-1 mm thick), markedly basally constricted, heavily corticated to their apices, bearing slender, irregularly branched ramelli ... *S. squallida* (p. 229)
2. Ultimate branchlets slender (under 1 mm thick), not or only slightly basally constricted, cortication only on older branches, with ramelli either one per segment or verticillate 3
3. Ramelli one per segment, 35-65 μ m thick, nodal bands 2-3 cells broad ... *S. filamentosa* (p. 222)
3. Ramelli becoming verticillate (1-6), 20-40 μ m thick, nodal bands 1 cell broad *S. tasmanica* (p. 227)

Spyridia filamentosa (Wulfen) Harvey 1833: 336; 1844: 449; 1846, pl. 46; 1855a: 537; 1859: 329; 1863, synop.: 42. J. Agardh 1852: 340; 1876: 268; 1897: 13. Boergesen 1917: 223, figs 222-226. Feldmann-Mazoyer 1940: 348. Guiler 1952: 98. Hommersand 1963: 177, figs 4-10. Hooker & Harvey 1847: 409. Krishnamurthy 1968: 42. Newton 1931: 394, fig. 236. Okamura 1932: 130. Reinhold 1897: 60. Sonder 1853: 680; 1880: 16. Tate

Fig. 1. *Spyridia filamentosa*. A. Pt Stanvac, S. Aust. (Lewis, 14.iv.1972; ADU, A41869). B. Female plant with young cystocarp (Pt Denison, W. Aust. Kraft, 14.xii.1971; ADU, A41175). C. Male plant with spermatangial ramelli (Aldinga, S. Aust. Cartledge, 30.iii.1972; ADU, A41815). D. Tetrasporangial plant (A41815).

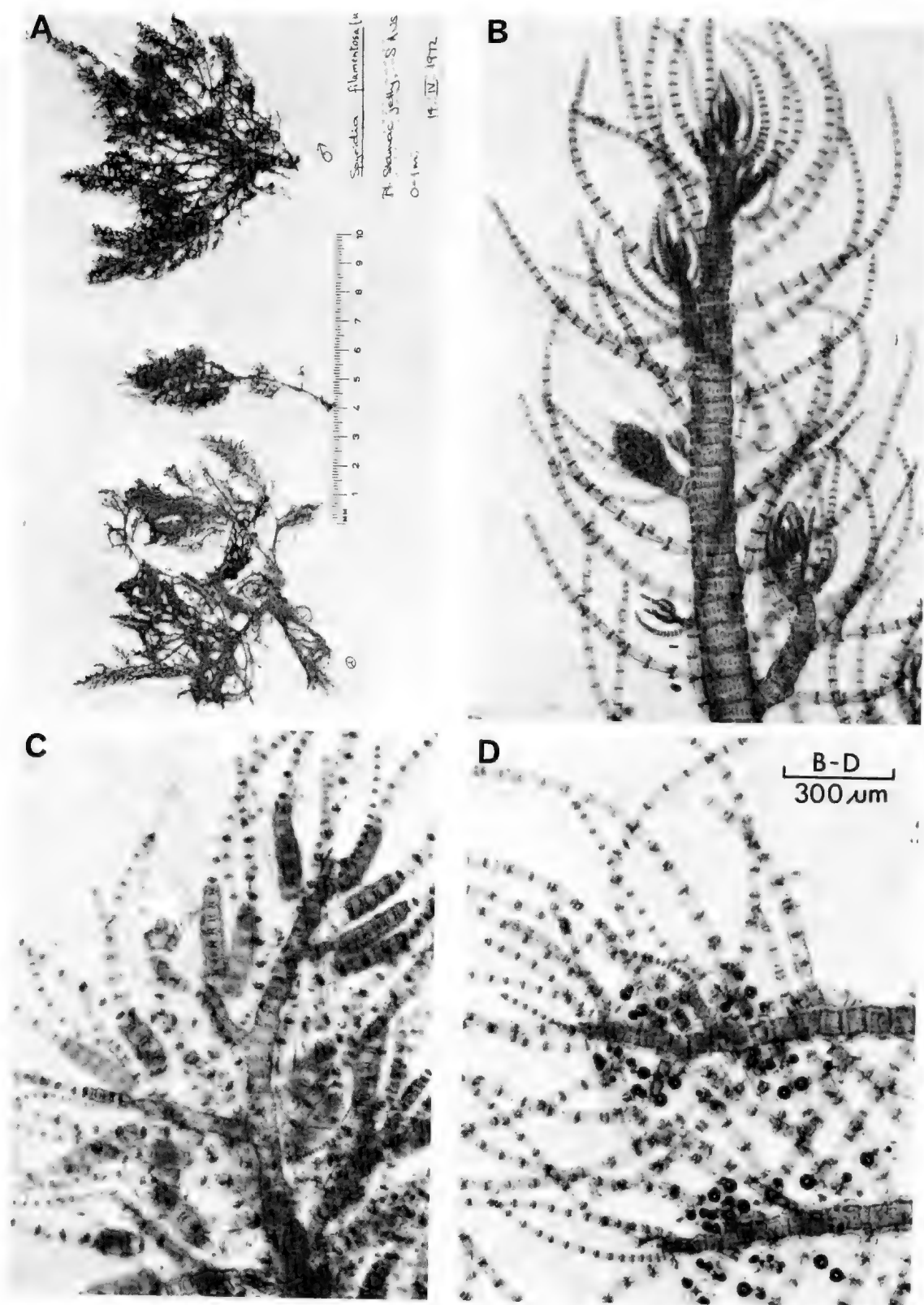


Fig. 1.

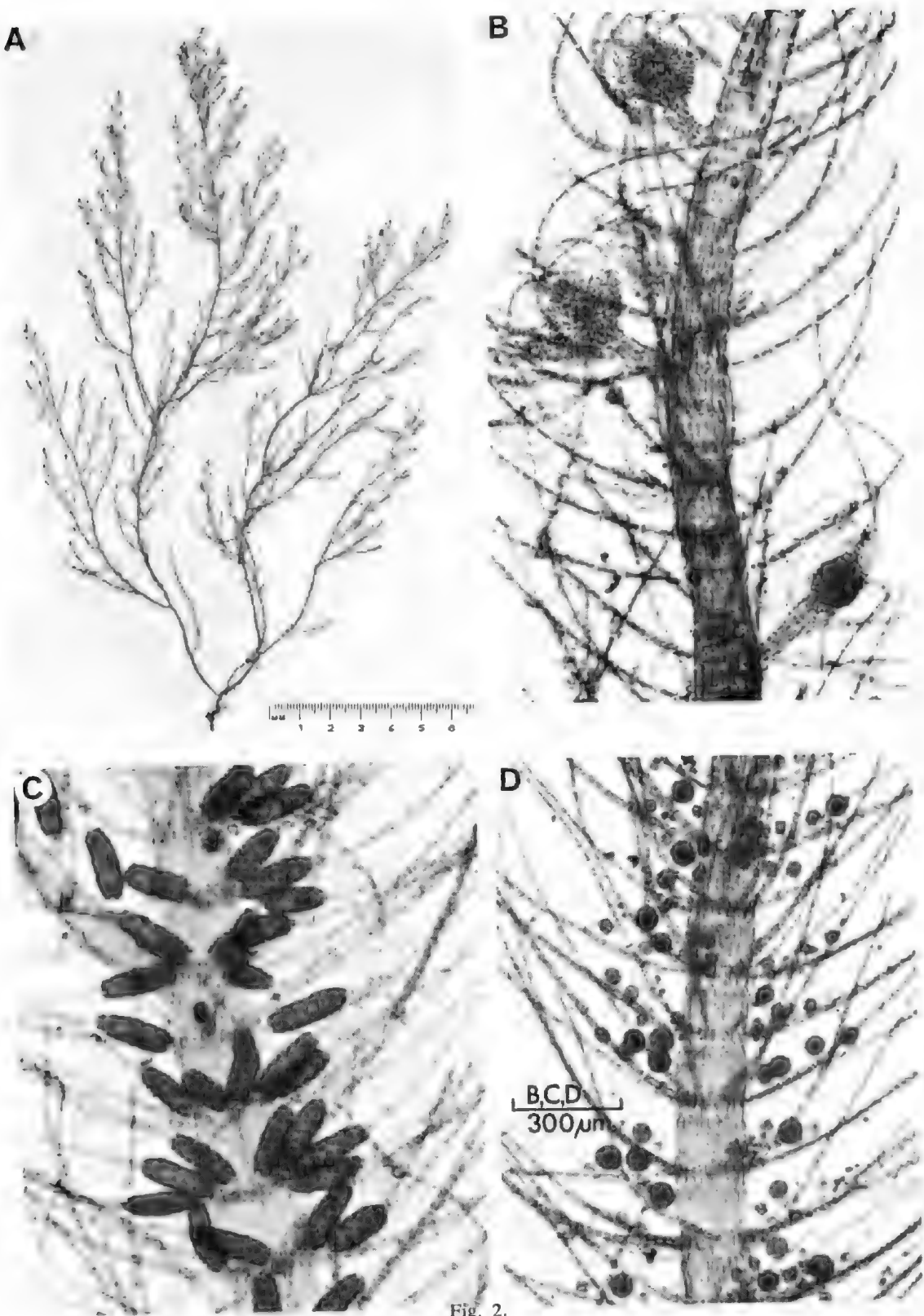


Fig. 2.

1882: 18. Tisdall 1898: 505. Wilson 1892: 181. Womersley 1958: 157.

Fucus filamentosus Wulfen 1803: 64.

S. filamentosa var. *arbuscula* Sonder 1855: 518. *S. biannulata* J. Agardh 1876: 267; 1897: 13. De Toni 1903: 1426. Guiler 1952: 98. Lucas 1909: 52; 1929a: 25; 1929b: 53. Lucas & Perrin 1947: 363. May 1965: 369. Okamura 1932: 130. Reinhold 1897: 60; 1899: 50. Sonder 1880: 16. Tisdall 1898: 505. Wilson 1892: 181. Womersley 1950: 180.

S. breviaristulata J. Agardh 1876: 268; 1897: 13. De Toni 1903: 1427. Guiler 1952: 98. Lucas 1909: 52; 1929a: 25; 1929b: 53. Lucas & Perrin 1947: 363. May 1965: 369. Okamura 1932: 130. Reinhold 1897: 60; 1899: 50. Sonder 1880: 16.

S. spinella Sonder 1845: 53; 1846: 168; 1880: 16. J. Agardh 1852: 342; 1876: 269; 1897: 13. De Toni 1903: 1430. Harvey 1863, synop.: 42. Kuetzing 1849: 668; 1862: 16, pl. 51c,d. Lucas 1909: 52. May 1965: 369. Mazza 1925, no. 824. Okamura 1932: 130.

FIGS 1, 3A, B

Thallus (Fig. 1A) usually 7–18 cm high, epilithic or epiphytic on various larger algae and seagrasses, lax and soft, irregularly much branched on all sides with longer and shorter branches intermixed, with one to several axes (often poorly defined) from an originally discoid holdfast, soon becoming fibrous or stoloniferous and entangled, commonly grey to grey-red, sometimes red-brown, in colour. Axes and larger branches corticated, terete; axes $\frac{1}{2}$ –1 (–1½) mm thick, tapering to branches 300–500 µm thick and branchlets 100–300 µm thick; laterals arising from periaxial cells or adventitiously from cortical cells. Segments usually clearly defined on branchlets (Fig. 1B), variable in length and proportions but usually (½)–1 times as long as broad, with bands of shorter nodal cells and longer internodal cells alternating; nodes with 11–14 periaxial cells, each corresponding to two internodal cells except for the (usually) larger periaxial cell bearing the ramellus. Cortication usually commencing a few mm from the apices but very variable, consisting of rhizoidal cells lying between the internodal cells and gradually forming a continuous cortex 1(–2) cells thick. Ramelli (Figs 1B, 3A, B) single per segment, irregularly spirally arranged, 1–1½ mm long with 12–20(–27) cells, linear or gently tapering apart from the terminal 2–3 very short

cells (Fig. 3A) which taper abruptly to a mucronate cell, (35–)40–55(–65) µm thick with cells (1½–)1½–2½(–3) times as long as broad; mucronate end cell often lost from older ramelli, ramelli with about 9 nodal cells, each usually cutting off 1(–2) cells anteriorly, giving a nodal band 2–3 cells broad.

Cystocarps (Fig. 1B) short-stalked, usually bilobed, lobes globular, 300–700 µm across.

Spermatangia covering the lower (except basal) several segments of ramelli (Fig. 1C), forming male organs 75–120 µm in diameter.

Tetrasporangia (Fig. 1D) sessile, 1–3 per cell on lower cells of ramelli, mostly on the upper (adaxial) side, spherical, 50–75 µm in diameter, tetrahedrally divided.

Type locality: Adriatic Sea.

Type: ?

Distribution: All around the Australian coast (including Tasmania) in conditions of moderate to slight wave movement.

Spyridia filamentosa is recognised as a widely distributed species, having been recorded from most seas, and many authors (e.g. Harvey 1846, pl. 46; Feldmann-Mazoyer 1940, p. 348) refer to it as a very variable species. J. Agardh (1876, p. 268) in segregating two Australian species (*S. biannulata* and *S. breviaristulata*) from *S. filamentosa*, referred to their similarity in habit with *S. filamentosa* and the large number of forms classed as this species. J. Agardh apparently regarded his two segregate species with some doubt, and a detailed study of extensive collections of Australian material does not provide any satisfactory way of segregating *S. biannulata* and *S. breviaristulata* from *S. filamentosa*.

The type of *S. biannulata* is from Tasmania (Georgetown, Tas., Gunn, LD, 51300, selected as lectotype) and was distinguished by J. Agardh in having more conspicuous bands of nodal and internodal cells and being less corticated above. *S. breviaristulata* is based on specimens from Whitsunday I., Queensland (lectotype in LD, 51311), and was distinguished by having the nodal and internodal bands short and of almost equal length. The variation in *S. filamentosa* encompasses the above features of both *S. biannulata* and *S. breviaristulata*.

Fig. 2. *Spyridia tasmanica*. A. Portarlington, Vic. (Wollaston, 17.viii.1956; ADU, A20567). B. Female plant with young cystocarps (Investigator Strait, S. Aust., 33 m deep, Watson, 24.i.1971; ADU, A41066). C. Male plant with spermatangial ramelli (Tapley Shoal, S. Aust., 15 m deep, Shephard, 2.ii.1969; ADU, A33538). D. Tetrasporangial plant (A41066).

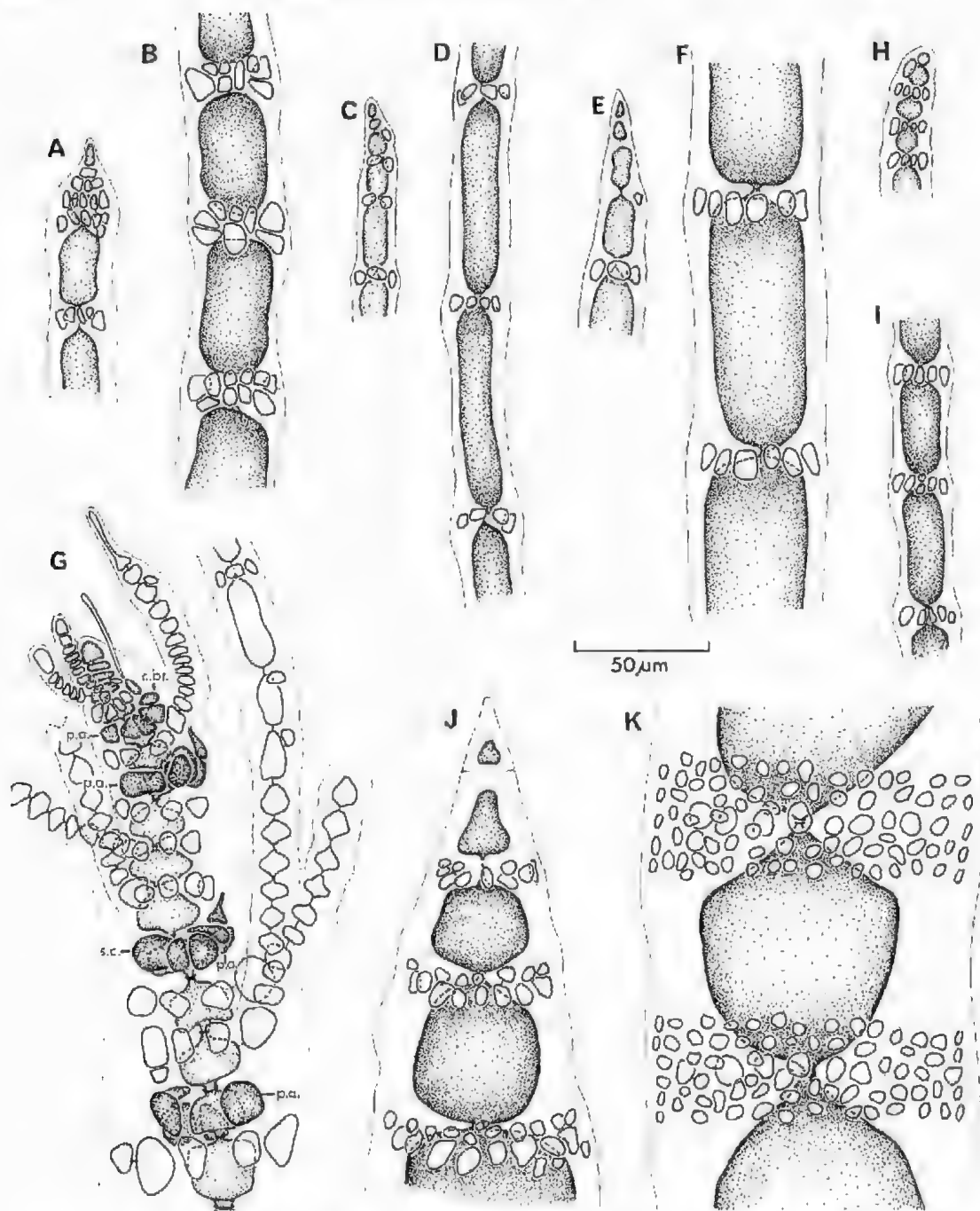


Fig. 3. *A, B. S. filamentosa*. Apex and mid region of ramellus, with periaxial cells in face view (A41815).
C, D. S. tasmanica. Ditto (A41066).
E, F. S. tasmanica. Ditto, robust form (A37622).
G. S. tasmanica. Female axis with procarys. (Gt Taylor Bay, Bruny I., Tas., 10 m deep. *Shepherd*, 7.ii.1970; ADU, A35287). c.br.—carpopogon branch; p.a.—periaxial cell; s.c.—supporting cell.
H, I. S. squalida. Apex and mid region of ramellus, with periaxial cells in face view (A26375).
J, K. S. dasyoides. Ditto (A20170).

S. filamentosa var. *arbuscula* Sonder (1855, p. 518) from Wilsons Promontory, Vic., May 1853 (type in MEL, 45181) is typical of the species and not a distinct variety.

S. spinella Sonder (type in MEL, 502090) was based on Preiss material from Western Australia. The type has somewhat broader and stouter ramelli than most specimens of *S. filamentosa*, with cells about as long as broad and the nodal bands of the ramelli 2–3 cells broad. Collections from Cottesloe, W. Aust., reef pools (Parsons, 14.xi.1968; ADU, A34072) and from Elliston, S. Aust. (Womersley, 15.i.1951; ADU, A15142) agree well with the type in having densely aggregated ramelli 400–800 μm long, composed of 15–18 cells, 50–65(–90) μm thick and 1–1½ times as long as wide. This is within the extremes of *S. filamentosa* and is probably typical of plants occurring in rock pools subject to moderate to considerable water movement. These plants are much closer to typical *S. filamentosa* than the Brest specimen discussed below, and are provisionally placed under *S. filamentosa*, but further studies on this "spinella" form and its variation are desirable.

S. filamentosa has been studied by several authors, most recently by Feldmann-Mazoyer (1940, p. 348), Hommersand (1963, p. 183) and Krishnamurthy (1968, p. 42). The Australian material agrees well with these descriptions, and also with material from Leghorn, Italy (Sartoni, 18.viii.1973; ADU, A43938). However, material from Brest, France (Cabiocch, Dec. 1972; ADU, A43050) has distinctly more robust ramelli (about 100 μm thick, cells scarcely longer than wide) which have 2–3 very small basal cells with the parent periaxial cell not enlarged, in contrast to the full-sized basal cells and enlarged periaxial cell of typical *S. filamentosa*. These two collections indicate that there may be greater variability in European *S. filamentosa* than in the Australian material.

Hommersand (1963) and Krishnamurthy (1968) differ in some details in their accounts of reproduction in the material they studied, as mentioned above in the introduction. Australian material (e.g. Aldinga, S. Aust. Cartledge, 30.iii.1972; ADU, A41881) shows three periaxial cells in fertile segments, but clarification of immediate post fertilisation stages has not been possible. No clear stages have been observed of a tetrasporangium arising directly from the axial cell of a ramellus (Hommersand 1963, p. 194), but it appears more likely that

periaxial cells are usually transformed into tetrasporangia. The number of periaxial cells in a ramellus does vary slightly, so it is not possible to state as Hommersand does that tetrasporangia must arise directly from the axial cell because the number of periaxial cells is the same in sterile or fertile segments.

***Spyridia tasmanica* (Kuetzing) J. Agardh 1852:**
342. Gordon 1972: 39. Harvey 1859:
329. Kuetzing 1862: 14, pl. 42 c, d.
Sonder 1853: 680.

S. filamentosa var. *tasmanica* Kuetzing 1849: 666.

S. filamentosa var. *verticillata* Harvey 1844: 449.

Wrangellia setigera Harvey 1859: 309, pl. 191A; 1863, synop.: 27. J. Agardh 1876: 622; 1879: pl. 32, fig. 3. De Toni 1897: 133; 1924: 149. Gordon 1972: 39. Guiler 1952: 99. Lucas 1909: 23; 1929a: 16. May 1965: 365. Mazza 1919, no. 678. Okamura 1932: 133. Sonder 1880: 29. Tisdall 1898: 511. Wilson 1892: 170.

FIGS 2, 3C-G, 4A-C

Thallus (Fig. 2A) usually 8–25 cm high, irregularly much branched, epilithic or on *Amphibolis*, with a small, discoid holdfast, grey-red to red-brown in colour. Branching irregularly alternate, branches terete, with one to a few main axes and prominent lateral branches, bearing lesser branches and branchlets on all sides, with whorled ramelli. Axes 1–1½(–2) mm thick, branches about ½ mm thick, lesser branchlets 200–400 μm thick. Segments (½–)¾–1½ times as long as broad (Fig. 2D), with usually 12 periaxial cells, each producing two internodal cells; cortication by rhizoidal cells from the nodal cells, commencing within 1–2 cm of apices and becoming heavy on axes and main branches. *Ramelli* (Figs 2D, 3C–F) 1(–3) per node near apices, becoming whorled (3–6(–8) per whorl with the addition of adventitious ramelli), arising from enlarged periaxial cells, ¾–2 (–3) mm long with 20–30 (–35) cells of greatest diameter (15–)20–35 (–40) μm and 3–5 times as long as broad, the end cell mucronate; robust form with ramelli (12–)15–20 cells long, greatest diameter 30–40(–45) μm and 1½–2½ times as long as broad. Ramelli with a single row of 8–14 nodal cells (Fig. 3D, F).

Cystocarps (Figs 2B, 4A) terminal on a short branchlet bearing ramelli, ½–¾ mm in diameter.

Spermatangia cover 2–6 cells (Figs 2C, 4B) within 1–2 cells of base of ramellus, forming a cylindrical male organ 70–130 μm in diameter and 1–6 times as long as broad.

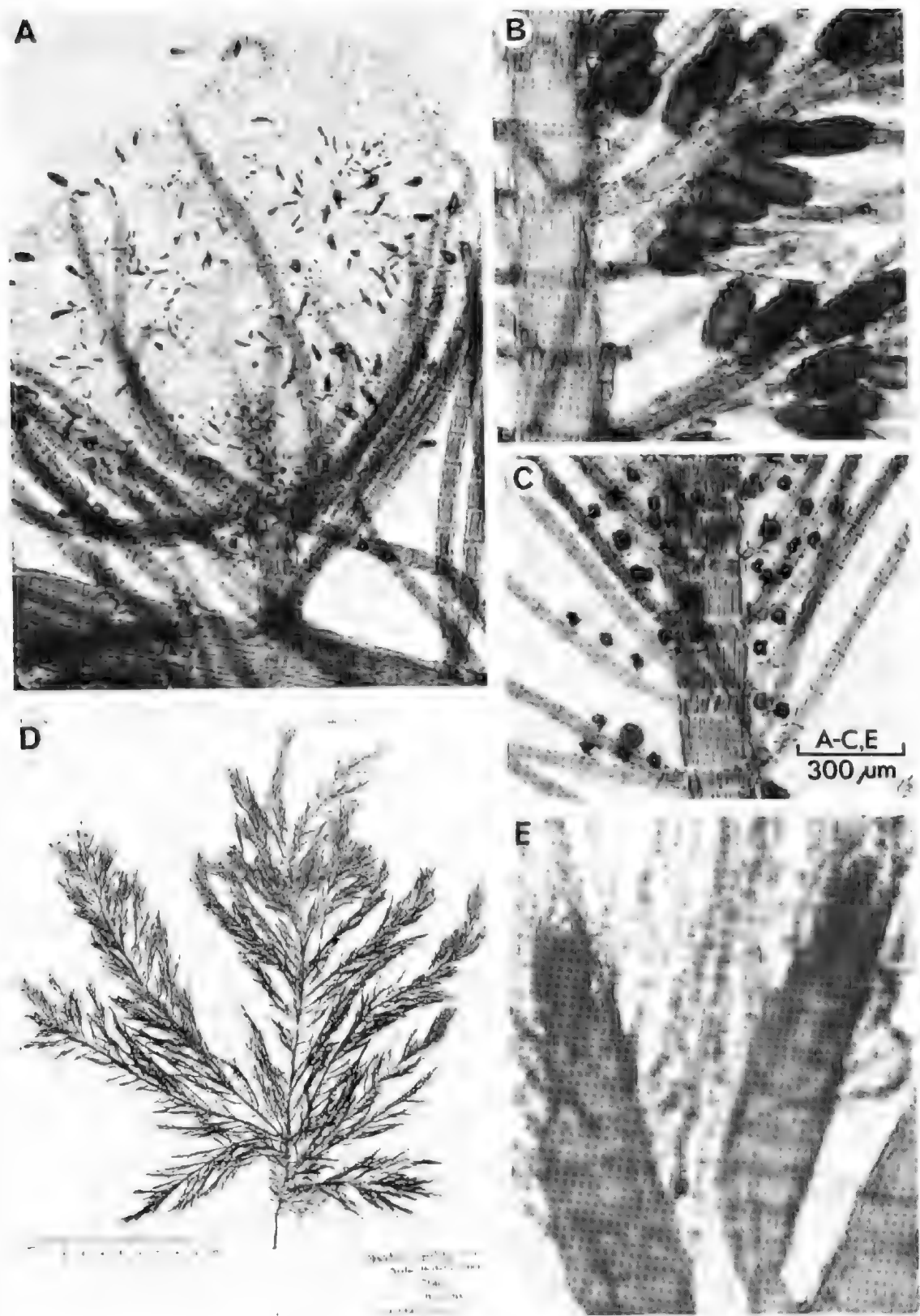


Fig. 4.

Tetrasporangia (Figs 2D, 4C) on 1–4 cells near the base of the ramelli, borne mostly on the upper (adaxial) side, 60–100(–120) μ m in diameter when mature, tetrahedrally divided.

Type locality: Tasmania (probably *Gunn*, ex *Hooker*).

Type: L. (941, 311...371).

Distribution: From Elliston, S. Aust. to Western Port, Vic. and around Tasmania. Generally in relatively calm localities, often with considerable current, 2–35 m deep, occasionally in partly sheltered habitats and shaded rock pools on rough-water coasts.

Development of reproductive structures in *S. tasmanica* appears to be very similar to that in *S. filamentosa*. The female axes (Fig. 3G) arise as short laterals and bear up to 5 procarys, separated by one or two sterile segments each with eight periaxial cells, one of which bears a ramellus. Each procary consists of 3 (rarely 4) periaxial cells, one of which is the supporting cell bearing the 4-celled carpogonial branch. Immediate post-fertilisation stages have not been clearly followed, but usually two groups of gonimoblast cells develop, probably from fusion cells originating from auxiliary cells cut off from the supporting cell and one of the other fertile periaxial cells. Sterile pericarp filaments arise from the periaxial cells of segments above and below the procary-bearing segment, forming a cystocarp similar to that in *S. filamentosa*.

Development of spermatangia and tetrasporangia is similar to that in *S. filamentosa*.

S. tasmanica is a distinctive species with its whorled ramelli and single row of nodal cells. The ramelli are typically slender (20–35 μ m thick), with mature cells 3–5 times as long as broad. However, some plants from rougher-water localities [e.g. Elliston, S. Aust., 7 m deep (*Shepherd*, 20.x.1970; ADU, A37622) and Cape Lannes, S. Aust., in shaded pool (*Kraft*, 12.ii.1972; ADU, A41809)] have more robust ramelli, 30–40(–45) μ m thick (Figs 3E, F, 4B, C) and mature cells 1½–2½ times as long as broad. Otherwise the latter specimens are similar to the majority of plants, and the type, of *S. tasmanica*, and the more robust, shorter-celled ramelli are regarded as

more characteristic of plants found under rougher-water conditions. Further studies on this form are, however, desirable.

Spyridia squalida J. Agardh 1876: 270; 1897: 16. De Toni 1903: 1436. Lucas 1909: 52; 1929b: 53. Lucas & Perrin 1947: 364. May 1965: 369. Okamura 1932: 130. Reinbold 1897: 60. Sonder 1880: 16. Tate 1882: 18.

S. wilsonis J. Agardh 1897: 16. De Toni 1903: 1435. Lucas 1909: 52. Lucas & Perrin 1947: 364. May 1965: 396. Okamura 1932: 130.

S. valida Sonder 1880: 16 (nomen nudum).

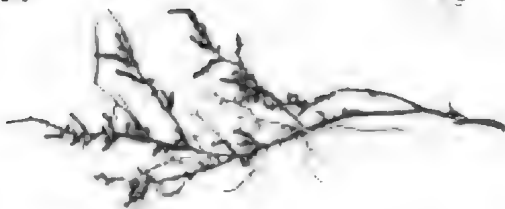
FIGS 3H, I, 4D, E

Thallus (Fig. 4D) usually 10–30 cm high, robust, erect, irregularly and proliferously branched, epilithic with one to several axes from a small discoid holdfast, usually with long, much branched, laterals on all sides, grey-red to red-brown in colour and when dried often appearing somewhat farinaceous. All branches terete and corticated to their apices, axes and main branches linear, branchlets (Fig. 4E) basally constricted and bearing densely arranged ramelli, especially on their upper parts, sometimes denuded below. Axes 1½–2½ mm thick, denuded below or with short, proliferous branchlets, tapering slightly to branches 1–1½ mm thick and lesser branchlets ½–1 mm thick. Segments largely obscured by cortication, ½–⅓ as long as broad, with 16 periaxial cells and about twice as many internodal cells; cortication commencing within a few axial cells of apices, pseudo-parenchymatous, 2–3 cells thick on branchlets, several cells thick on axes. Ramelli (Figs 3H, I, 4E) one per segment close to apices and derived from periaxial cells, but scattered adventitious ramelli (usually) densely cover the branchlets, sometimes persisting onto larger branchlets; ramelli ½–1(–1½) mm long with (10–)14–20(–24) cells of greatest diameter (20–)30–40(–45) μ m and (1–)1½–2(–2½) times as long as broad. Ramelli with a single row of small nodal cells (Fig. 3I) derived from 5–6 periaxial cells each of which cuts off 2–3 outer cells in the same transverse plane.

Cystocarps short-stalked, globular-bilobed, 1–4 mm in diameter.

Fig. 4. *Spyridia tasmanica* (robust form). A. Female plant with squashed mature cystocarp (Elliston, S. Aust., 7 m deep in bay. *Shepherd*, 20.x.1970; ADU, A37622). B. Male plant with spermatangial ramelli (A37622). C. Tetrasporangial plant (A37622). *Spyridia squalida*. D. Victor Harbor, S. Aust. (*Womersley*, 18.iii.1966; ADU, A30032). E. Branchlets and ramelli (Pt Elliot, S. Aust. *Dodd*, 12.iii.1963; ADU, A26375).

A



C



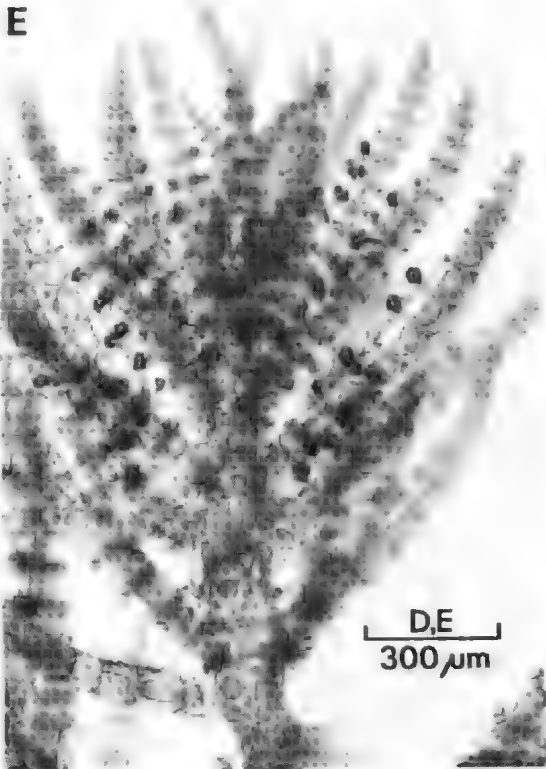
B



D



E



D,E
300 μ m

Fig. 5.

Spermatangia cover the lower 2–6 cells (except basal cell) of ramelli, forming a male organ 50–80 μ m in diameter.

Tetrasporangia borne on the lower several cells of the ramelli, largely on the upper (adaxial) side, 1 (–2) per cell, sessile, spherical to slightly ovoid, 40–60 μ m in diameter when mature, tetrahedrally to sub-crucially divided.

Type locality: "Nov. Holland. australem".

Type: Herb. Agardh, LD, 51533.

Distribution: From Geographe Bay, W. Aust. to Waratah Bay, S. Gippsland, Vic., usually in deep water (2–24 m deep).

Female axes of *S. squalida* develop as short, adventitious branchlets which are more heavily corticated than in other species but less so than in vegetative branchlets of this species. Alternating segments each bear a procarp, with the sterile segments bearing ramelli. Usually three periaxial cells occur in fertile segments, one (the supporting cell) producing a 4-celled carpogonial branch. Two, or probably often 3, auxiliary cells are formed, leading to a carposporophyte with two or three lobes. The pericarp develops similarly to that in other species.

S. squalida is a distinctive and robust species of *Spyridia*, having cortication to the apices and thus forming swollen, basally-constricted, branchlets, bearing ramelli often densely scattered but usually soon denuded. The farinaceous appearance is also a common feature of older, dried plants.

S. wilsoni J. Agardh is typical *S. squalida*. The type of the former is from Pt Phillip Hds, Vic. (J. B. Wilson, 1887: LD 51532), and the thallus is not compressed as stated by J. Agardh (1897) and May (1965).

S. valida Sonder (1880: 16) is a nomen nudum, based on a specimen in MEL (45195) from Geographe Bay, W. Aust. (Bunbury, 1875), accompanied by Sonder's drawings. It is typical *S. squalida*.

S. squalida was recorded from Port Alfred (Kowie), South Africa by Barton (1896, p. 196), and the record repeated by De Toni (1903, p. 1436) and Lucas & Perrin (1947, p. 364). This record almost certainly applies to some other species, probably to *S. plumosa* Schmitz ex J. Agardh (G. F. Papenfuss, pers. comm.).

Spyridia dasyoides Sonder 1853: 680; 1880: 16. J. Agardh 1876: 272. De Toni 1903: 1437. Harvey 1863, synop.: 42. Lucas 1909: 52. Lucas & Perrin 1947: 364. May 1965: 369. Okamura 1932: 130. Tate 1882: 18. Tisdall 1898: 505.

S. opposita Harvey 1855b: 256; 1860: pl. 158. Adams 1972: 83. J. Agardh 1876: 270; 1897: 14. De Toni 1903: 1431; 1924: 502. Guiler 1952: 98. Lucas 1909: 52; 1929a: 25; 1929b: 53. Lucas & Perrin 1947: 363, fig. 182. May 1965: 369. Mazza 1912, no. 421. Okamura 1932: 130. Reinbold 1897: 60. Shepherd & Womersley 1970: 135. Sonder 1880: 16. Tate 1882: 18. Tisdall 1898: 505. Wilson 1892: 181. Womersley 1950: 180; 1966: 151.

S. prolifera Harvey 1863: pl. 274. J. Agardh 1876: 269; 1897: 14. De Toni 1903: 1431. Lucas 1909: 52. Lucas & Perrin 1947: 362, fig. 181. May 1965: 369. Mazza 1912, no. 422. Sonder 1880: 16.

FIGS 3J, K, 5

Thallus (Fig. 5A–C) usually 10–20 cm high, erect, epilithic or epiphytic, much branched with one to several axes from an originally discoid holdfast which soon becomes fibrous and stoloniferous, dark red to red-brown in colour. Axes and larger branches heavily corticated, terete to angular and becoming four-sided with thickened cortical flanges in line with the 4 ranks of ramelli, densely branched. Axes 1–2 (–2½) mm thick, often denuded but sometimes with numerous, short, proliferous branchlets, tapering to branches ½–¾ mm thick and lesser branchlets ¼–½ mm thick; branching usually subdistichous (Fig. 5C) with laterals arising from nodal cells. Segments largely obscured by cortication, 1–1½ times as long as broad, with 8 periaxial cells producing 16 internodal cells and the 8 cells soon with interposed rhizoidal cells giving both nodal and internodal rings of 16 cells (Fig. 5D); cortication commencing within a few segments of apices, of elongate cells later appearing pseudo-parenchymatous, a few cells thick on branchlets, many (especially on flanges) cells thick on axes. Ramelli (Figs 3J, K, 5D, E) arising from an enlarged periaxial cell, in opposite and more or less decussate pairs (Fig. 5D) on successive segments (often displaced to two rows on each side in the plane of branching), (1–)1½–2(–2½) mm long with (16–)18–22 cells, relatively uniform

Fig. 5. *Spyridia dasyoides*. A. Holotype (MEL, 45128). B. Robe, S. Aust. (Cartledge, 14.v.1972; ADU, A42174)—an irregularly branched form. C. Investigator Strait, S. Aust., 43 m deep (Watson, 27.i.1971; ADU, A38143)—distichously branched form. D. Branch showing arrangement of ramelli (Pt Denison, W. Aust. Kraft, 14.xii.1971; ADU, A41730). E. Ramelli with tetrasporangia (Vivonne Bay, Kangaroo I., S. Aust. Womersley, 30.i.1956; ADU, A20170).

in diameter and tapering fairly abruptly to a point. (70–)100–150 μm thick, cells about 1(–1.1) times as long as broad. Ramelli with 16–20 nodal cells, each cutting off 1–2 cells (which often divide again) on both sides (anteriorly first), producing a nodal band (2–)3–5 (–6) cells broad (Fig. 3J, K).

Cystocarps short-stalked, irregularly globular to bilobed, 400–600 μm in diameter.

Spermatangia cover the lower (except basal) several segments of young ramelli of adventitious branchlets lying between older ramelli, forming male organs 120–200 μm in diameter.

Tetrasporangia (Fig. 5E) sessile, 1–3 per cell, mostly on the upper (adaxial) side of the ramelli, subspherical, 50–90 μm in diameter, tetrahedrally divided.

Type locality: Holdfast Bay, S. Aust. (F.v. Mueller).

Type: MEL, 45128.

Distribution: From Port Denison, W. Aust. to Gabo I., Vic. *S. dasyoides* usually occurs on rough-water coasts from low tide level to depths of 33 m. Deeper growing plants are usually more delicate than those growing in turbulent conditions.

The reproductive cells develop very similarly to those in *S. filamentosa* or *S. tasmanica*. Female axes correspond well with that illustrated (Fig. 3G) for *S. tasmanica*, having alternating sterile and procarpic segments, with the latter comprising a 4-celled carpogonial branch on the supporting cell and usually two other periaxial cells. The mature cystocarp encloses two or three discrete carposporophyte lobes and the pericarp is relatively firm at its periphery.

S. dasyoides is characterised by its robust, opposite and more or less decussate ramelli, with cells about as long as broad and nodal bands 3–5 cells broad, together with the largely distichous branching. Eight periaxial cells are formed in branches and soon become separated

by rhizoidal cells, thus forming both nodal and internodal rings of usually 16 cells, the bands being about equal in length.

The type of *S. dasyoides* (Fig. 5A) in MEL is typical of this species, previously known mainly as *S. opposita*. Sonder's hand-written label with the holotype gives the locality as "Adelaide", inland from Holdfast Bay. The type of *S. opposita* (in TCD) is from Preservation Harbour, on the south-west coast of the south island of New Zealand (Lyal, Jan. 1851), and agrees very well with the southern Australian plants. Adams (1972, p. 83) records *S. opposita* from several localities near Wellington, New Zealand, and although it is apparently not widely known in New Zealand, the specimens (e.g. CHR, 55775, from Patu-rangi, Nelson) agree well with Australian material. The type of *S. prolifera* Harvey, in TCD, is from Fremantle, Western Australia (Clifton), and is a plant with denuded branches bearing proliferous branchlets. *S. prolifera* represents older plants of *S. dasyoides*, where the thick axes and branches are probably remnants of the previous years' growth, from which numerous short branchlets have arisen proliferously. The structure of the ramelli is identical with that of *S. dasyoides*. Plants referred to *S. prolifera* are apparently not infrequent on the Western Australian coast, where younger and typical plants of *S. dasyoides* also occur.

Acknowledgments

The first author gratefully acknowledges a grant from the Australian Research Grants Committee and the technical assistance provided by Mrs Enid Robertson and Miss Cheryl Anderson. Dr G. Sartoni, Istituto Botanico, Firenze, Italy, and Dr J. Caboche, Station Biologique de Roscoff, France, kindly made available material of *S. filamentosa* from Europe. The Director of the National Herbarium, Melbourne, is thanked for the loan of specimens.

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OBITUARY: GRAHAM FREDERIC WHITTEN, M.SC.

BY P. B. WEBB

Summary

OBITUARY

GRAHAM FREDERIC WHITTEN, M.Sc.

16.IV.1924-16.III.1975

Graham Whitten, former Deputy Director of Mines in South Australia died on 16 March, 1975, after a long illness. With his passing the State lost an outstanding geologist.

Whitten graduated as B.Sc. from the University of Queensland in 1946 and subsequently joined the Electrolytic Zinc Company where he worked as geologist and later Senior Geologist at the Rosebery Mines in Tasmania. After several years at Rosebery, he became responsible for exploration for the company in Tasmania, New South Wales and Queensland.

In 1954 he accepted an appointment as Senior Geologist in the Geological Survey Division of the South Australian Department of Mines. He was promoted in 1965 to Supervising Geologist and during the next five years was responsible for all activities of the Exploration Services Division, and in 1970 was appointed Chief Geologist.

With the untimely death of the then Acting Director of Mines, Dr K. R. Miles, in March 1972, Whitten was left in administrative control of the entire Department for a period of eight months. He was subsequently appointed Deputy Director, the post which he held until

his premature retirement due to serious illness, in November 1973.

Whitten made a significant contribution towards the understanding of the iron formations of South Australia. In relation to this work he visited Europe and North America in 1958 and 1967, and was awarded an M.Sc. degree from the University of Adelaide.

He was elected Fellow of the Society in 1962 and was Secretary from 1970-72. He played a prominent part in the affairs of the Geological Society of Australia and was also an active member of the Australasian Institute of Mining and Metallurgy. He was also a member of the Society of Economic Geologists and of the Society of Exploration Geophysicists (U.S.A.).

His energy and drive will be remembered by all who were privileged to know and to work with him. His many official reports and published papers are a fitting record of his career.

To his wife Betty and to his three daughters, we offer our deepest sympathy. He will be sadly missed by his professional associates and by his many personal friends.

B. P. WEBB.

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Printed by Graphic Services Pty Ltd, 88a Pirie Street, Adelaide 5000